

---

# QUATERNARY ENVIRONMENTAL HISTORY AND AGRICULTURAL IMPACT ON VEGETATION IN CENTRAL AMERICA

---

Dolores R. Piperno<sup>1</sup>

## ABSTRACT

The corpus of historical data from lake sediments relating to the climate, vegetation, and human land use of the lowland Central American tropical forest between ca. 20,000 BP and the time of European contact is reviewed. Pollen, phytolith, and charcoal records identify the distribution and composition of tropical vegetation and fire patterns during the late Pleistocene, when they were significantly altered from today's, and earliest Holocene, when plant communities reassembled and interglacial representatives began to coalesce on the landscape. The significance of the environmental perturbations that occurred during the transition from the Pleistocene to the Holocene for human occupation of the lowland tropical forest and the geography and chronology of agricultural origins is discussed. Fire was employed by hunters and gatherers and farmers alike during the past 11,000 years as a primary tool of forest modification. The profound effects of an ancient pre-Columbian development of plant food production and, subsequently, slash and burn agriculture between ca. 10,000 BP and 1000 BP can be seen on lowland forests from Mexico to the Amazon Basin.

*Key words:* Climate, human land use, prehistoric agriculture, Quaternary history, seasonal tropical forests, slash and burn cultivation, vegetation.

## RESUMEN

Se revisa la recopilación de datos históricos de sedimentos lacustres que conciernen el clima, la vegetación y la utilización humana del suelo de los bosques tropicales de tierras bajas de América Central entre ca. 20,000 A.P. y el momento de contacto europeo. Registros de polen, fitolitos y carbón identifican la distribución y composición de la vegetación y los patrones de fuego durante el Pleistoceno tardío, cuando fueron marcadamente alterados en relación al presente y al inicio del Holoceno, cuando las comunidades de plantas se reasociaron y los representantes interglaciales comenzaron a unirse en el paisaje. Se discute el significado que las perturbaciones ambientales durante la transición del Pleistoceno al Holoceno tuvieron en la ocupación humana del bosque tropical de tierras bajas, y la geografía y cronología de los orígenes agrícolas. El fuego fue empleado por cazadores y recolectores y granjeros por igual durante los últimos 11,000 años como una herramienta primaria de la modificación del bosque. Los efectos profundos de un antiguo desarrollo pre-colombino de la producción de plantas alimenticias y, posteriormente, de la agricultura de tala y quema entre ca. 10,000 AP y 1000 AP pueden verse en los bosques de tierras bajas desde México hasta la cuenca amazónica.

---

This paper presents a summary of Late Pleistocene and Holocene environmental conditions in the Central American lowland tropical forest. Natural and human-caused changes in vegetation and climate that occurred during the past 20,000 years are discussed with reference to the accumulated evidence acquired from botanical and minerological studies of lake sediment cores. Insights that historical data may provide about how to best conserve and restore tropical forests are also outlined. I focus primarily on paleoecological records that date to the Late Pleistocene and early Holocene periods. Debates surrounding vegetation and climate in the tropical forest during that time have been fervent and long-standing, but now appear to be converging on a consensus with regard to some important issues. I do not provide a systematic overview of the Holocene-

aged records for climate change now available from lower elevations of Central America. The quality and quantity of information dating to the past 10,000 years are rapidly increasing, and it is beyond the scope of this paper to cover it (see Grimm et al., 2001, for an excellent review, including the burgeoning literature on the timing and effects of past ENSO (El Niño/Southern Oscillation) cycles). I do attempt to provide a more thorough examination of the evidence for past human influences on the lowland tropical forest—including a discussion of a few of the most important records from South America—from the initial stages of colonization, through the earliest periods of agriculture, until the arrival of Europeans. The reader should nonetheless bear in mind that it is possible to cite but a small fraction of the associated archaeological literature generated during the past 20 years.

---

<sup>1</sup> Smithsonian Tropical Research Institute, Panama, and Department of Anthropology, National Museum of Natural History, Washington, DC. pipernod@si.edu



Paleoecological data attesting to the considerable changes in climate and vegetation that impacted the lowland Neotropical forest during ice ages have accumulated primarily during the past 25 to 30 years. Before that, because direct empirical information was very limited, theories of environmental stasis dominated questions concerning tropical forest ecology and environmental history, including explanations of species diversity (e.g., Fisher, 1960; Slobodkin & Sanders, 1969). These theories were elegant, and at the time they made a good deal of sense because it was logical to assume that the presence of a constantly warm and wet climate over millions of years would promote a continuous accumulation of species while creating little stress on the existing biota and causing only low rates of extinction.

At about the same time that theories of long-term tropical environmental stability held influence, what would become a famous archaeological debate was developing over the importance of ancient human occupations in the tropical forest. The dry highland regions of Mesoamerica and South America, where the (then) best understood and most famous high civilizations had arisen in the New World, were viewed by some prominent prehistorians as the major sources of most pre-Columbian cultural innovations and advances, including crop plant origins, pottery manufacture, and large and permanent village settlements (e.g., Mangelsdorf, 1953; Mangelsdorf et al., 1964; Meggers, 1954, 1971). Skepticism abounded in these circles as to whether the tropical forest was a fit environment for human habitation and innovation, including the development of effective agricultural systems (Mangelsdorf, 1953; Meggers, 1954, 1971; see Sauer, 1950, 1952, and Lathrap, 1970, 1973a, for the alternative viewpoint that tropical forest cultures *had* been very important). Some scholars would argue into the 1980s that the first people to colonize Central and South America largely avoided tropical forest, and that they and later tropical hunters and gatherers could not have survived for long without access to a cultivated food supply because wild food resources were scarce (e.g., Hart & Hart, 1986; Bailey et al., 1989; Sponsel, 1989).

Consequently, the degree to which cultural forest modification had taken place during the pre-Columbian era was in serious question. The "Ecologically Noble Savage" concept that tropical forest peoples lived in harmonic balance with their natural resources, minimally disrupting the landscapes on which they settled, was in full, politically-correct swing (see Alvard, 1993, and Dods, 2002, for a good discussion of the Noble Savage concept in anthropology and its historical antecedents). Descriptions of the extant tropical forest as "pristine" floral communities

practically untouched by the human hand were common in both the anthropological and ecological literature.

During the 1960s and 1970s, pioneering studies by Van der Hammen and Gonzalez (1960), Livingstone (1975), and Martin (1964) provided the first empirical data demonstrating that highland regions occupying tropical latitudes in Africa and America experienced dramatic climatic and vegetational changes at the same time periods during which glaciations were strongest in higher latitudes of the Northern Hemisphere. These investigations, along with a now-classic application of environmental reconstruction through palynology in the Classic Maya area (Deevey et al., 1979), motivated similar research in the lowland tropics. Lakes with sediments rich in pollen and phytoliths that dated to the past 20,000 years, and thus that could provide evidence on the most extreme climatic oscillations of the last transglacial cycle, occurred more commonly in lowland tropical forest than was originally thought (e.g., Leyden, 1984, 1985; Bush & Colinvaux, 1988, 1990; Bush et al., 1989, 1992; Piperno et al., 1990). The furious constructions of modern reference collections of pollen and phytoliths that accompanied these initial paleolimnological efforts would lead to the identification of many of the lacustrine plant microfossils at more precise taxonomic levels than had been thought possible. It became clear that robust reconstructions of past environments through the same types of paleolimnology that had long been pursued in Europe and North America were achievable in the lowland tropical forest.

Also beginning in the 1970s and 1980s, archaeologists began to intensify their explorations in the tropical forest by investigating new areas and increasing their coverage of others. These efforts included carrying out intensive foot surveys using statistically significant sampling designs that not only identified more early human occupations, but also robustly documented regional trends in site number and size and population density through time (e.g., Cooke & Ranere, 1984; Lathrap et al., 1975). In addition, new and rigorous methods were applied to recover and study plant and other organic cultural remains (Pearsall, 1978; Piperno, 1985a, b, 1988). Traditional methods, such as the analysis of visible remains of seeds, fruits, and nuts, had not worked in studying early plant use and domestication and, indeed, were providing highly biased pictures of human plant exploitation because organic materials do not survive for long under the inimical warm and humid conditions found in the tropics. Our understanding of the natural and human processes affecting the lowland Neotropical forest during the



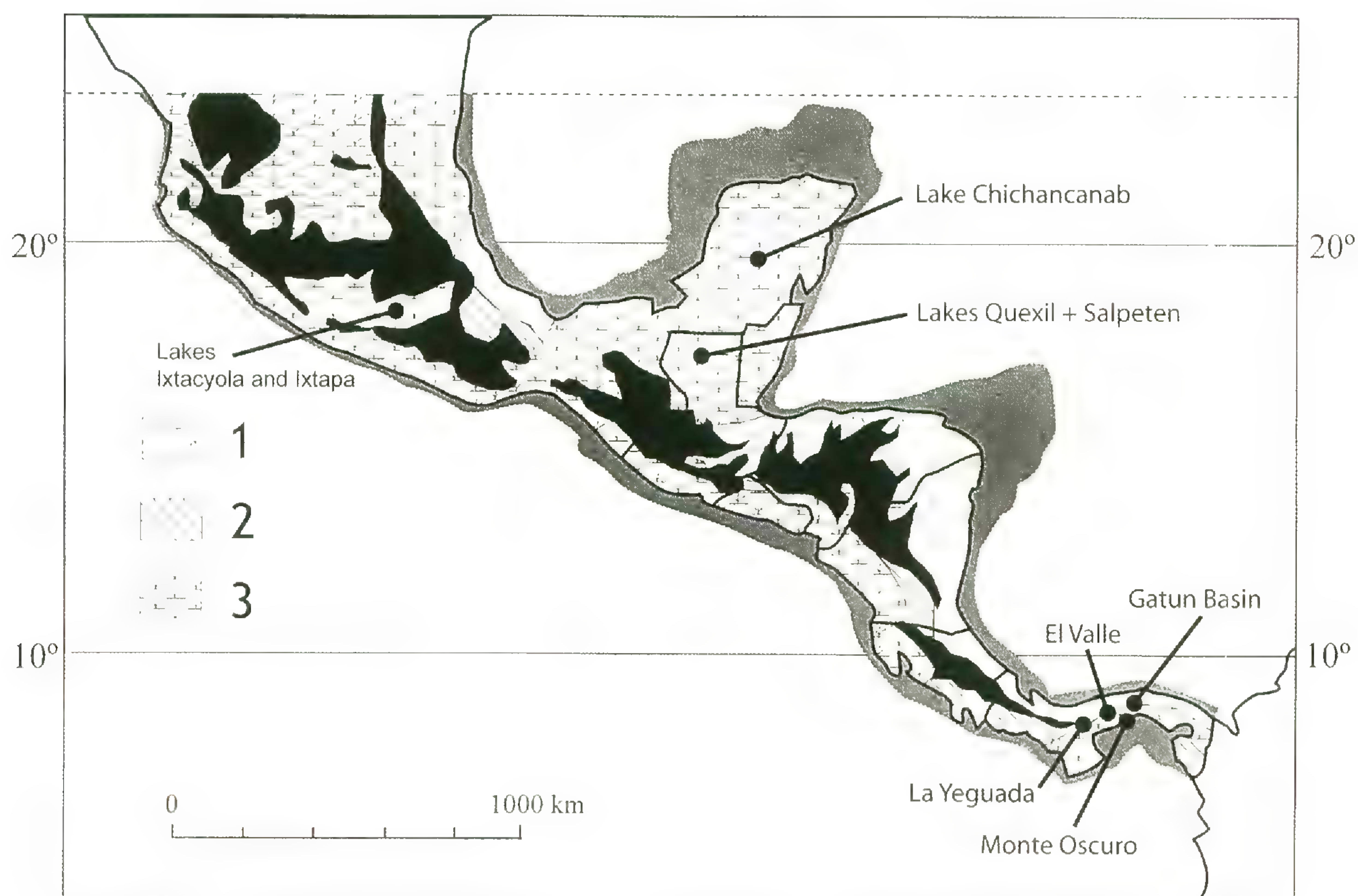


Figure 1. Location of paleoecological sites with records dating to the Pleistocene and the reconstructed vegetation of lowland tropical Middle and Central America between 20,000 BP and ca. 10,500 BP. Gray areas represent land exposed by lowered Pleistocene sea levels at 18,000 BP, the period of maximum glacial advance. Black areas indicate elevations above 1500 m asl. Modified from Piperno and Pearsall, 1998: fig. 2.4, with permission from Elsevier. Sites and their investigators are as follows: Lake Chichancanab (Hodell et al., 1991); Lake Quexil (Leyden et al., 1993); Lake Salpeten (Leyden, 1987); La Yeguada (Piperno et al., 1990, 1991a; Bush et al., 1992); El Valle (Bush & Colinvaux, 1990; Piperno et al., 1991a); Gatun Basin (Bartlett & Barghoorn, 1973; Piperno et al., 1992); Monte Oscuro (Piperno & Jones, 2003); Lakes Ixtacyola and Ixtapa (Piperno, this paper, and Piperno et al., 2004). The vegetational reconstruction is as follows: (1) Largely unbroken moist forest, often with a mixture of presently high-elevation and lowland forest elements. In some areas, montane forest elements (e.g., *Podocarpus* L'Hér. ex Pers., *Quercus*, *Alnus* Mill., *Ilex*) were conspicuous. Annual precipitation was lower than today, but sufficient precipitation existed to support a forest. (2) Forest containing drier elements than characteristic today. High-elevation forest elements occurred, especially in moister areas of the zone. Areas near the 2000 mm precipitation isohyet and areas with sandy soils may have contained savanna woodland. The vegetation may have been patchy. (3) Mostly undifferentiated thorn woodland, low scrub, and wooded savanna vegetation. Some regions (e.g., Guatemala) had temperate elements (e.g., *Juniperus*). Areas receiving greater than 2000 mm of rainfall today may still have supported a drier forest, as in (2). River- and stream-side locations supported a forest.

past 20,000 years and more has been dramatically altered as a result of the above-mentioned work.

#### LATE PLEISTOCENE VEGETATION AND CLIMATE

Most existing lake records of Late Pleistocene age from the Americas, including the tropics, date to not more than 20,000 to 25,000 years ago (all ages in the paper are in uncalibrated radiocarbon years). The bulk of the available data are, however, of an age appropriate for evaluating the problems addressed here because the final 10,000 years of the last transglacial cycle (between about 20,000 and 10,000 BP (before present)) has long been a period of intense interest to paleoecologists and archaeologists alike. It covers the Last Glacial Maximum (18,000 BP) and

subsequent termination of the Pleistocene, and accommodates all now-accepted chronologies for human colonization of the Americas (Dillehay, 1997, 2000; Meltzer, 1997; Meltzer et al., 1994). Furthermore, although paleoecological records from the now-humid lowlands are still few in number, they originate from a representative spectrum of the major ecological zones found in the lowland Neotropics from ever-wet, aseasonal habitats to those characterized by a marked seasonality of rainfall.

Figure 1 shows the locations of the major lakes and large swamps in Central America that have yielded records dating to the Pleistocene period. Vegetational and other reconstructions derived from these paleoenvironmental sequences were often based on pollen, phytolith, diatom, and mineralogical data analyzed in



tandem. Figure 1 also contains a postulated reconstruction of vegetation for the Central America lowlands during the late-glacial period. For areas where sequences of Pleistocene age do not yet exist, I assumed the paleovegetation to be similar to the paleovegetation in areas which are presently similar ecologically.

The major environmental trends and patterns indicated from the records have been described in detail elsewhere (e.g., Bush et al., 1992; Leyden et al., 1993; Piperno & Pearsall, 1998) and are summarized herein. The lowland Neotropics between 20,000 and 10,000 BP appear to have been considerably cooler and drier than they are today. Reconstructions of tree line descent indicate that temperatures over land surfaces were from 4°C to 7°C lower than at the present time; these estimates are largely concordant with those derived from newer studies of Pleistocene sea surface temperatures derived from coral oxygen isotopes (Bush et al., 1992; Colinvaux et al., 1996; Guilderson et al., 1994; Leyden et al., 1993; Peltier & Solheim, 2004). The degree to which the Pleistocene precipitation was reduced is under considerable discussion. Many of the lakes shown in Figure 1 were lower or completely dry during the Late Pleistocene and, as will be described shortly, many of their watersheds appear to have contained few trees. These factors have led many investigators, the author included, to believe that intertropical annual rainfall was probably reduced on the order of about 30% to 50% (Leyden, 1984; Leyden et al., 1993; Piperno & Jones, 2003; Van der Hammen & Hooghiemstra, 2000). Others would disagree, believing that rainfall reduction was instead only about 10% to 15% below today's values (e.g., Colinvaux et al., 1996, 2000).

There is no doubt that glacial-age atmospheres contained much less CO<sub>2</sub> than they would after the Pleistocene ended (Barnola et al., 1987; Cowling & Sikes, 1999). CO<sub>2</sub> concentrations were 33% lower than preindustrial values (PIV) until ca. 12,500 BP, when they were still 25% lower than the PIV, not rising close to PIV values until about 9000 BP (Barnola et al., 1987). The lower CO<sub>2</sub> concentrations probably exerted significant influences on the vegetation in ways we do not understand very well at present (Cowling & Sikes, 1999; Mayle & Beerling, 2004). One possible major effect was that Pleistocene forest canopies were more open than today's due to lower light use efficiency during photosynthesis (Sage, 1995).

In many regions of the tropics these identified ice age conditions—much cooler, probably substantially drier, and with much lower atmospheric CO<sub>2</sub>—persisted until 12,000 to shortly after 10,500 years ago, such that modern vegetation communities did not

begin coalescing until that time. For example, at Lake Quexil, located in the Peten, Guatemala, seminal work by Barbara Leyden and her colleagues (Leyden, 1984; Leyden et al., 1993) showed that trees now characteristic of the modern semi-evergreen forest in the region are not recorded in pollen records until a short time after ca. 10,300 BP, and that it took at least another several hundred years before a well-developed tropical forest was established. During the Late Pleistocene, in contrast, the region was a cool and very dry place in which few trees grew.

Existing paleoecological data allow us to identify the following major, Late Pleistocene vegetational patterns. First, where the modern potential vegetation is deciduous or drier forms of semi-evergreen forest, a replacement of forest is evidenced by open vegetation similar to but probably not exactly equivalent with today's thorn woodlands, thorn scrublands, and savanna. This is empirically demonstrated in the lowlands of southwest Mexico, Guatemala, Haiti, and Pacific-side Panama, at Lakes Ixtacyola, Ixtapa, Quexil, Salpeten, and Monte Oscuro. Second, where today the annual rainfall is between about 2.6 and 4 m and the actual or potential vegetation is evergreen and semi-evergreen forest, the Pleistocene vegetation was largely forested. This is empirically demonstrated in Caribbean-side Panama at the Gatun Basin, as well as at Pacific watershed sites in Panama at elevations of between 500 and 700 m above sea level (asl), such as La Yeguada and El Valle. This situation presumably prevailed throughout the Caribbean watershed of Central Panama and other low lying wetter areas as well. At the middle elevation sites (ca. 500–1000 m asl) where the Pleistocene vegetation was forest (e.g., El Valle, La Yeguada), it can be seen particularly well how the arboreal component of the vegetation responded to the cooler temperatures; trees that today generally grow only in mountainous areas above 1500 m were forced about 800 to 1200 m downslope and co-existed with those lowland arboreal elements that were better at tolerating lower temperatures.

It is not surprising in view of all of this that few to none of the vegetational signatures from the Pleistocene appear to have modern analogues. There were different forest facies likely involving the reduction and partial replacement of lowland evergreen forest by arboreal elements now primarily confined to drier types of forest. However, because species-specific tree identifications usually cannot be made from pollen and phytolith records, details of forest composition are difficult to reconstruct with any certainty. This is an area of research where increasing our efforts to retrieve and identify seeds and other macro-fossil plant remains from lake sediments may prove to be rewarding.





Figure 2. The crater and surrounding rim of Monte Oscuro, Panama.

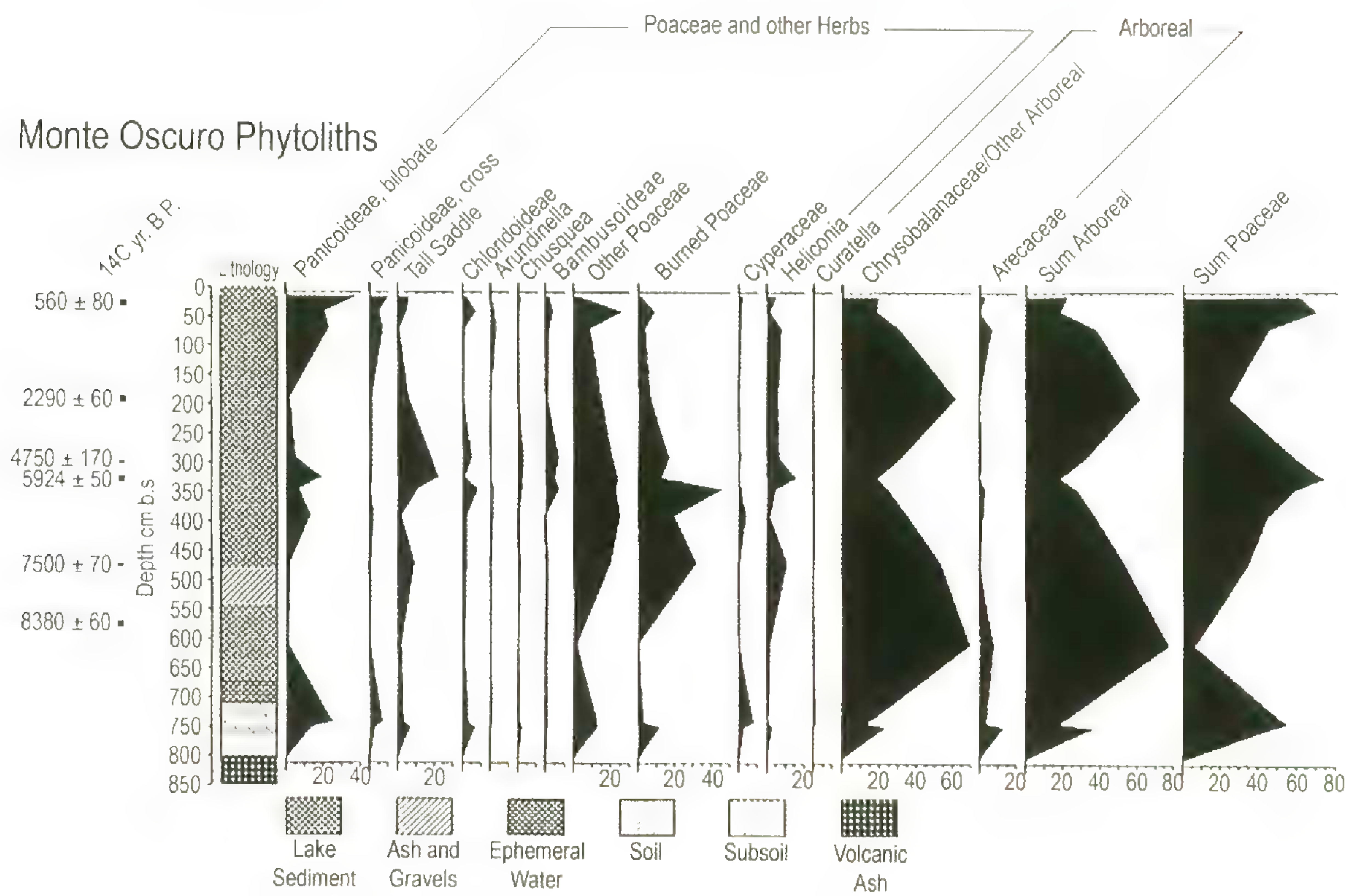


Figure 3. The percentage of each major phytolith taxon found at Monte Oscuro, Panama. The Chrysobalanaceae/Other Arboreal category contains predominantly Chrysobalanaceae phytoliths (usually > 85%–90%), with contributions also from *Protium*, other Burseraceae, the Moraceae, Euphorbiaceae, Annonaceae, Conmaraceae, and Flacourtiaceae. Percentages for burned Poaceae phytoliths were calculated separately. Only short cell phytoliths from grasses (e.g., bilobates, saddle-shapes) were studied for evidence of burning. Taxa attributions are as follows: *Chusquea* Kunth. (Poaceae). Reprinted from Piperno and Jones (2003), with permission from Elsevier.

The paleobotanical records from a few of these sites are now discussed in more detail to better illustrate the interpreted findings. The author and John Jones recently studied phytolith and pollen records from Monte Oscuro, Panama, a large lake located in an extinct crater 75 km west of Panama City where

annual rainfall presently is 1.8 m (Piperno & Jones, 2003; Figs. 2–4). This sequence is the first from Panama dating to the Pleistocene from the seasonally dry Pacific coastal plain, where the potential vegetation is a deciduous tropical forest and the forests, therefore, would be particularly prone to



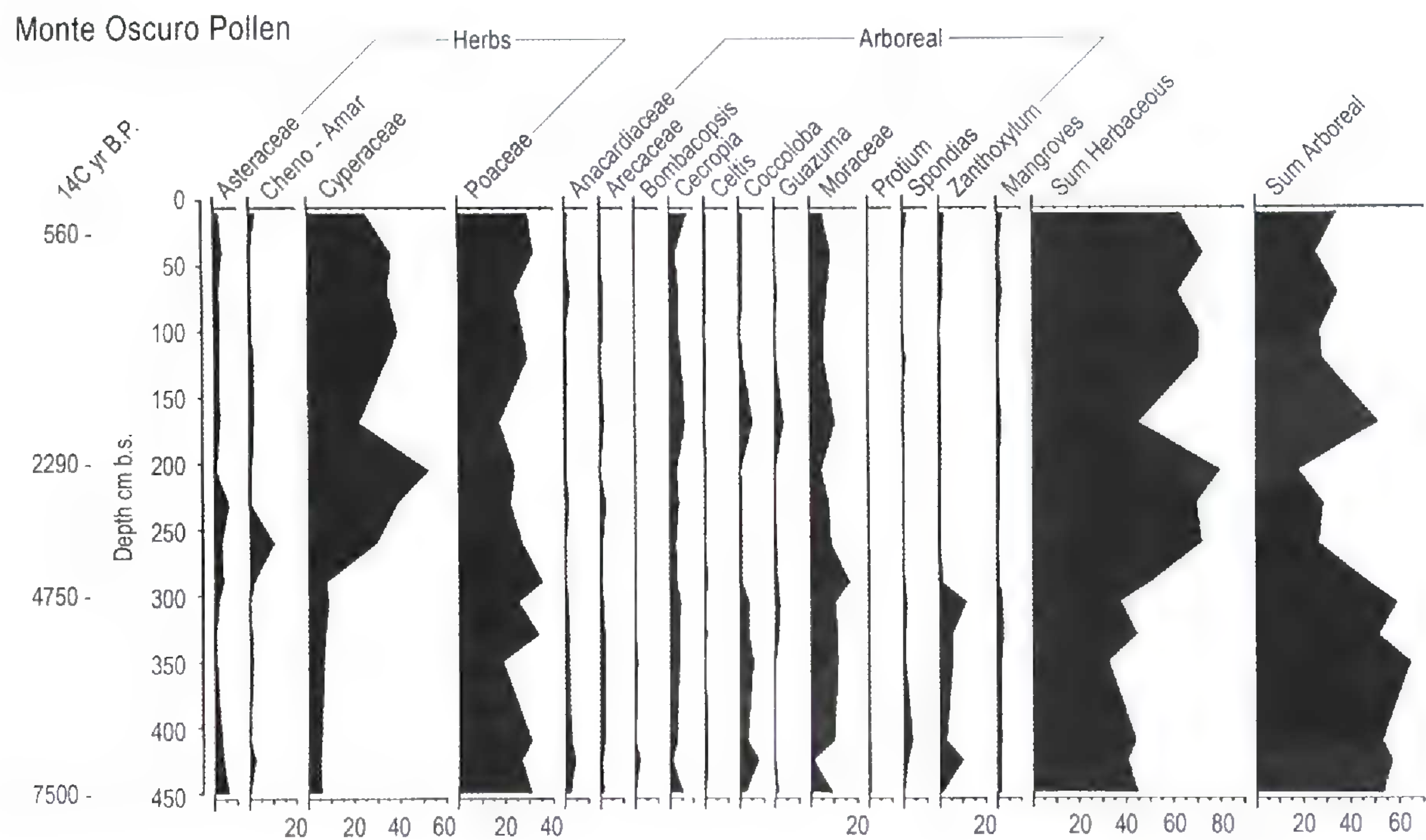


Figure 4. The percentage of each major pollen taxon found at Monte Oscuro, Panama. Cheno-Amar refers to Chenopodiaceae–Amaranthaceae. Taxa attributions are as follows: *Bombacopsis* (Bombacaceae) Pittier. Reprinted from Piperno and Jones (2003), with permission from Elsevier.

fragmentation under conditions of significant climatic drying. The sedimentary sequence from Monte Oscuro shows that during the Late Pleistocene the lake bed was persistently dry, such that a paleosol formed and supported an associated vegetation. Pollen is not preserved in these sediments because they were subjected to oxidation, but phytoliths are common.

The phytolith data from the paleosol indicate that during the Late Pleistocene, the Monte Oscuro region supported a vegetation containing many grasses, sedges, and other herbaceous plants (Fig. 3). The archetypal indicator of savanna in the Neotropics, the shrub or small tree *Curatella americana* L., is also present during this period. Trees that are characteristic of the modern deciduous forests of the area appear to have grown in low numbers. Grass phytolith morphology indicates that the Chloridoid (short grasses) and Panicoid (tall grasses) sub-families are common in the phytolith assemblages. These grasses predominantly use the C<sub>4</sub> photosynthetic pathway (only a small proportion of modern Panicoid grasses are C<sub>3</sub>), further adding to the picture of a dry and open landscape. Charcoal (not shown) and burned grass phytoliths (Fig. 3) also occur, indicating that the landscape was periodically subjected to fires. During this interval, arboreal phytolith taxa are represented mainly by the Chrysobalanaceae and Arecaceae. There are a few phytoliths from *Protium* Basm. f., the Annonaceae, and the Moraceae, indicating these trees were also growing nearby.

At an estimated date of ca. 10,500 BP (at a depth of 7m), a substantial water table rise and initial ponding occurred, leading to the establishment of a permanent

water body that lasted into the modern era. The date for the filling of the Monte Oscuro crater is consistent with the inundation of other lake beds in tropical America that were dry or much lower during the Late Pleistocene (Curtis et al., 1999; Ledru et al., 1998). Both the phytolith (Fig. 3) and pollen (Fig. 4) records show that during the early Holocene a diverse tropical deciduous forest expanded into the Monte Oscuro watershed. By 8300 BP, percentages of grass and sedge phytoliths had declined greatly from their Pleistocene occurrence frequencies and *Curatella* L. is no longer recorded at all. By shortly after 7500 BP, when sediments first contain high amounts of pollen, a number of trees occur in the pollen assemblages whose modern ecological affinity is seasonal tropical forest (e.g., *Zanthoxylum* L., *Spondias* L., *Protium*, *Bursera* Jack., *Erythrina* L., *Celtis* L., species of Anacardiaceae and Moraceae; other arboreal taxa such as *Trema* L., *Machaerium*-type, *Cavanillesia* Ruiz & Pav., and *Calophyllum*, which are not shown) (Fig. 4).

During the Pleistocene, the Monte Oscuro region supported open kinds of vegetation consisting of a large number and variety of herbaceous taxa, including grasses and sedges, and small shrubs and trees, including *Curatella* and palms, adapted to dry-land habitats. Trees that form important components of seasonal tropical forests in the region today were not entirely eliminated from the landscape but appear to have grown in low numbers. Some of them were probably growing along the margins of water courses. In light of these factors and the amount of modern annual precipitation the area receives, 1800 mm, it is



likely that annual rainfall in the Monte Oscuro region was reduced during the Late Pleistocene by at least 35%. It is also reasonable to extrapolate from the Monte Oscuro record to predict that a significant part of the Pacific coastal plain of the Panamanian land bridge was a dry and open habitat. It might be unwise, however, to use the word savanna to describe the Late Pleistocene vegetation. Thorny scrub associations (those with many legumes, cacti, and also some euphorbs) produce few phytoliths that can be identified even to the family level, and are thus difficult to document in phytolith records. It is likely that these types of plants were present on the landscape, perhaps in considerable number, and, along with the plant taxa that can be documented through their microfossils, formed species combinations that were well adapted to Pleistocene dry climatic phases but that do not at the present time grow together.

How heterogeneous and probably patchy the Pleistocene vegetation was across small distance scales in regions such as Panama, where one can move from tropical deciduous to tropical evergreen forest in a leisurely 90 minute car ride, is illustrated by the pollen and phytolith sequences from La Yeguada and El Valle studied by Mark Bush, Paul Colinvaux, and the author (Figs. 5, 6). These sites are located in the Pacific watershed uplands between 500 and 650 m asl (Fig. 1). They receive between 3 and 4 m of rainfall annually today, twice the amount as on the Pacific coastal plain where Monte Oscuro is located. The climate is still highly seasonal at these two sites; over 90% of the rain falls during the wet season and there is a long and marked dry season of five months' duration. In each case, the Pleistocene vegetation was a forest containing trees now found mainly at elevations of 1500 m and above, such as *Quercus* L., *Ilex* L., and *Magnolia* L. (Fig. 5). However, presence of the clay type illite—a mineral that typically forms when the soils and rocks of a lake's catchment are little weathered from rainfall—in the Pleistocene but not in the Holocene deposits at Lake La Yeguada (described in Bush et al., 1992) is a good indication that during the Late Pleistocene the region's precipitation was considerably less than today's. At El Valle, a surge in *Chenopodium* L. and *Alternanthera* Forssk. pollen between 19,000 and 12,000 BP indicates the lake contracted severely at that time, almost certainly a response to climatic drying (Fig. 6; Bush & Colinvaux, 1990).

The most recently generated data dating to the Pleistocene from the Central American lowlands, which are still in a preliminary state and cannot be discussed in detail here, come from the Central Balsas River Valley located in tropical southwestern Mexico, where

no information on the paleoenvironment was previously available. The author began a project there five years ago to reconstruct the environmental and cultural history of the region. This is where the extensive molecular work carried out by John Doebley and colleagues during the past 15 years places the origin of maize, whose ancestor they have determined to be a species of teosinte, *Zea mays* L. subsp. *parriglumis* Iltis & Doebley, native to the Central Balsas region (e.g., Doebley, 1990; Matsuoka et al., 2002; Fig. 7). As over much of the Pacific watershed of Central America, the potential vegetation of the region is a tropical deciduous forest. Preliminary information from two lakes, Ixtacyola and Ixtapa, located in and near the Iguala Valley on the eastern side of the Central Balsas region at an elevation of 700 m asl (Fig. 1) suggests that there, also, the Late Pleistocene climate was much cooler and drier than today's and the glacial vegetation contained fewer trees than did early Holocene associations (Piperno et al., 2004).

#### SUMMARY: WHAT HAVE WE LEARNED ABOUT PLEISTOCENE ENVIRONMENTS?

The Pleistocene climate in the lowland Neotropics is now understood to have been a peculiar combination of low temperature, precipitation, and atmospheric CO<sub>2</sub>. The cumulative effect of these conditions on tropical plant communities and whether all were effecting community structure and floristic composition to an equally significant degree, are under considerable discussion. It has been suggested that low CO<sub>2</sub> concentrations alone might explain much of the displacement of forest by herbaceous vegetation seen in the Pleistocene lake records from Central and South America (e.g., Colinvaux et al., 2000; Mayle & Beerling, 2004). In order to more closely study this issue, Huang et al. (2001) analyzed leaf wax carbon isotopes in lakes from Chihuahua, Mexico (Lake Babicora), and Peten, Guatemala (Lake Quexil). It is well understood that the Chihuahua and Guatemala regions were, respectively, fairly wet and very dry during the Late Pleistocene due to being under the influence of different sources of moisture. Today, the two regions still experience contrasting precipitation patterns, which are the opposite of what they were during late glacial times. Huang et al. (2001) were able to show conclusively that at Lake Babicora there was much more C<sub>3</sub> vegetation during the late-glacial period than during the Holocene. The opposite was true at Lake Quexil, where, in accordance with the palynological data indicating the presence of open, dry-land environments, the Late Pleistocene vegetation was shown to contain many more C<sub>4</sub> plants than did the Holocene vegetation. The wet climate that



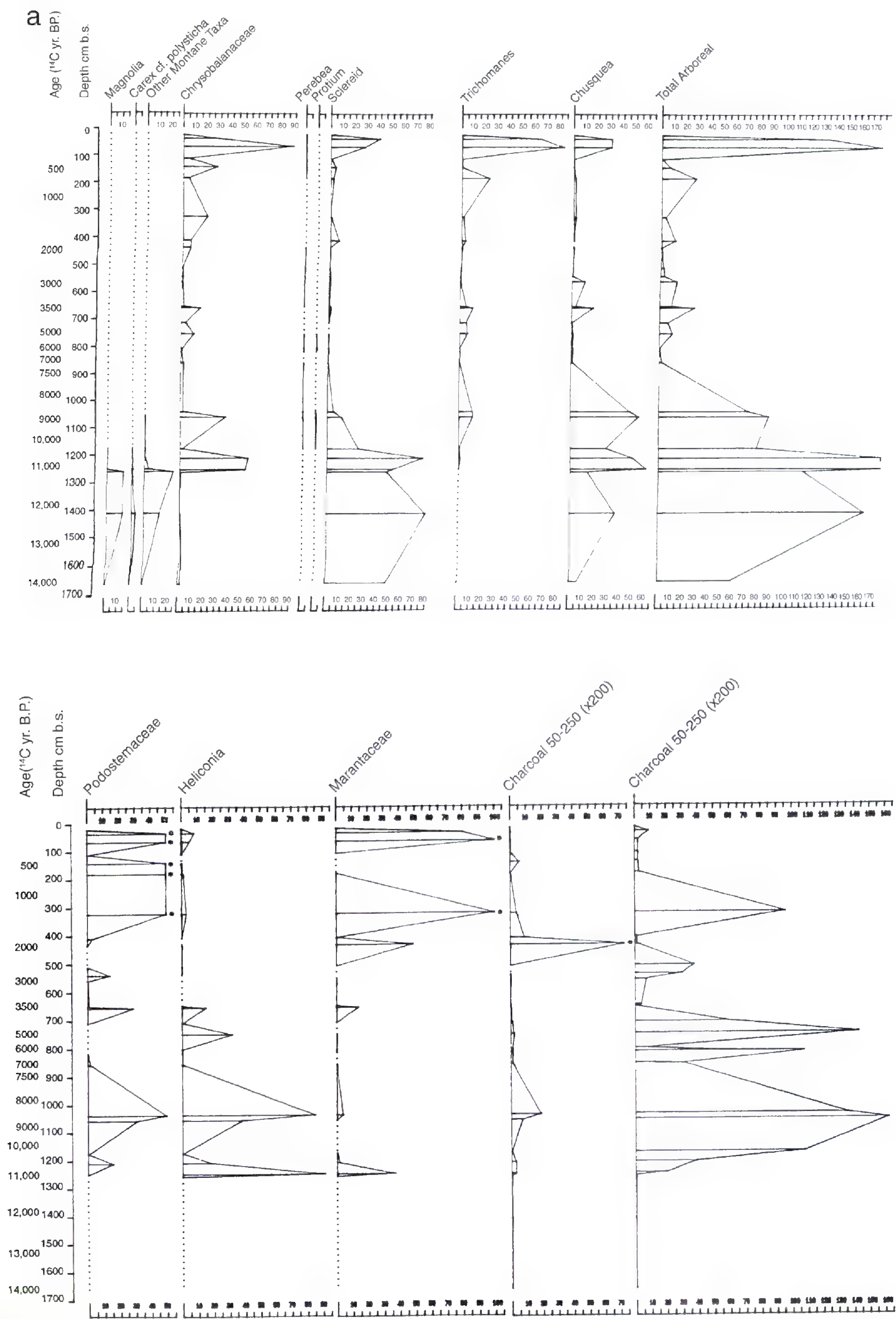


Figure 5a. A phytolith influx (number of phytoliths per 20 cm<sup>2</sup> per yr.) diagram from Lake La Yeguada, Panama. Taxa attributions are as follows: *Magnolia* L. (Magnoliaceae), *Carex* sp. ined. aff. *polysticha* Boeck (Cyperaceae), *Perebea* Aubl. (Moraceae), *Protium* Basm. f. (Burseraceae), *Trichomanes* L. (Hymenophyllaceae). From Piperno et al. (1991b).



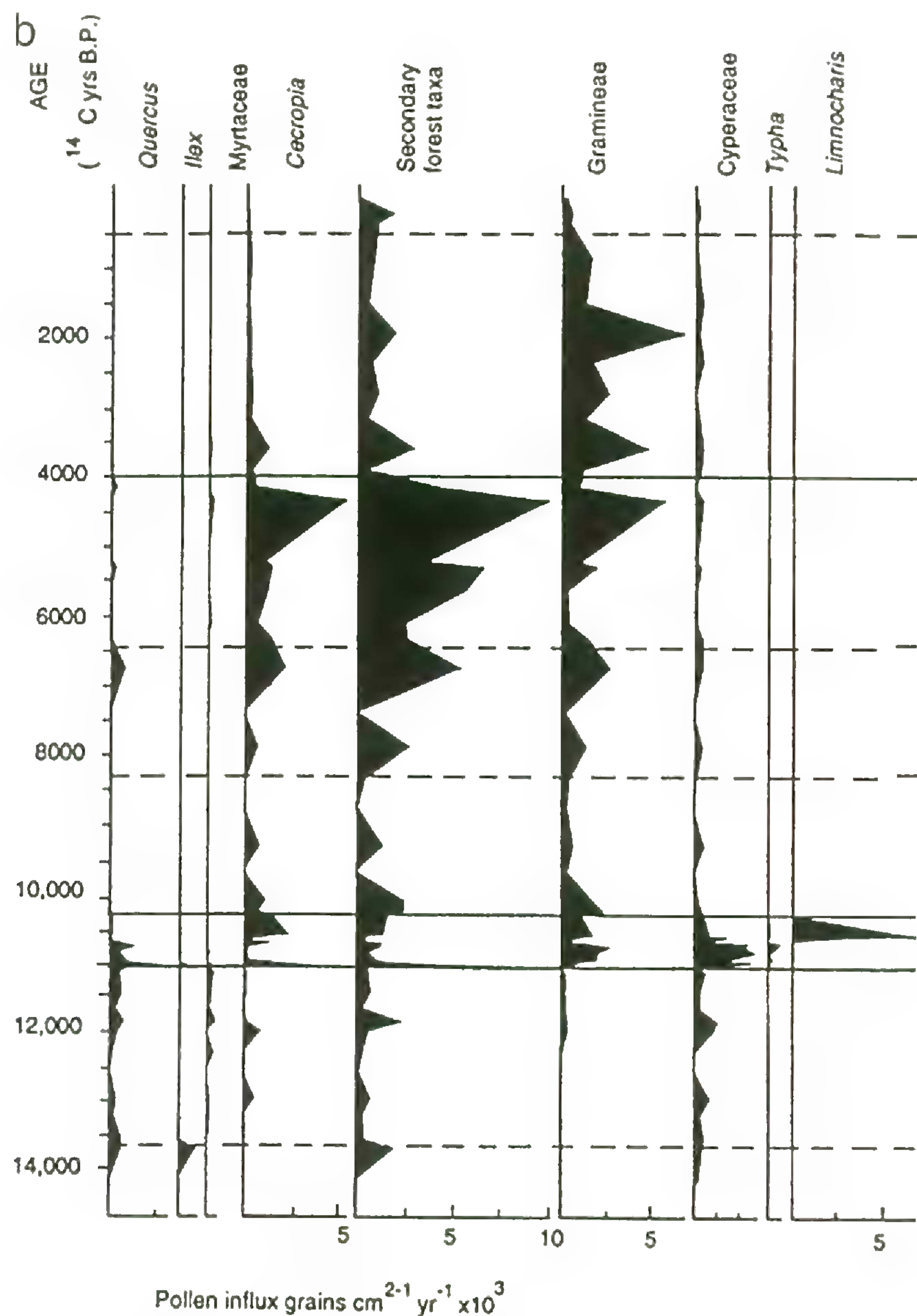


Figure 5b. A pollen influx (number of pollen grains per cm<sup>2</sup> per yr. × 10<sup>3</sup>) diagram from La Yeguada, Panama. Taxa attributions as follows: *Typha* L. (Typhaceae), *Limnocharis* Bonpl. (Butomaceae). From Piperno et al. (1991b).

prevailed at Lake Babicora thus had far more influence on the regional vegetation than the low atmospheric CO<sub>2</sub> concentrations did.

Therefore, vegetational shifts from C<sub>3</sub>-dominated forests to C<sub>4</sub>-dominated grasslands in the tropics cannot be driven without concurrent significant reductions in precipitation. Furthermore, low CO<sub>2</sub> concentrations acting largely separately from climatic influences probably cannot explain why many presently deep lakes from Mexico to southern Brazil were dry lake beds or shallow water bodies during the Late Pleistocene (e.g., Ledru et al., 1998; Leyden, 1984; Leyden et al., 1993; Piperno & Jones, 2003; Piperno et al., 2004) and why incontrovertible signals of substantially reduced precipitation, such as the evaporitic mineral gypsum and the clay illite, formed in some of them (Bush et al., 1992; Leyden et al., 1993). While low CO<sub>2</sub> may certainly have exacerbated drought stress and further promoted the expansion of C<sub>4</sub> and CAM open-land plants at the expense of some

C<sub>3</sub> forest species, the tropical ice age climate appears to have been substantially cooler and drier.

Formerly thought to be incompatible physical forces of the Pleistocene climate, cooling and drying can now be understood to have been mechanistically and causally linked. The negligible amount of evaporation that took place over cooler tropical ocean surfaces, for example, meant that much less water vapor was available to become rainfall over adjacent land surfaces (Webb et al., 1997). The persistence of forest in higher precipitation areas such as at La Yeguada and El Valle, even under what the author and others think was probably a 30% to 40% decline of precipitation, is not surprising because sufficient moisture would still have been available to support species-diverse forests. Furthermore, in these C<sub>3</sub>-dominated forests, cooler Pleistocene temperatures probably would have counter-balanced the effects of lower precipitation by improving carbon and water balance and reducing evapotranspiration gradients



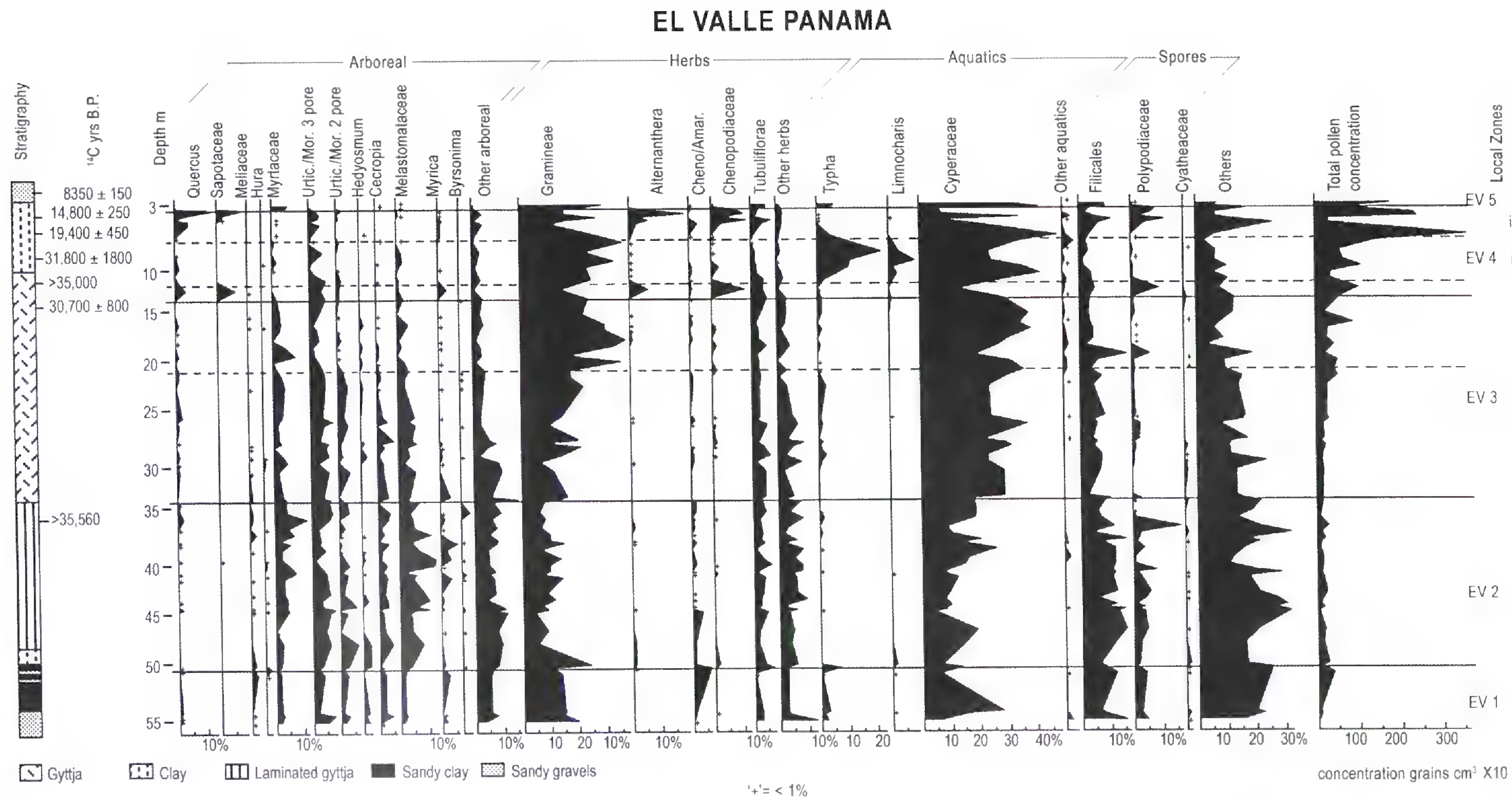


Figure 6. The percentage of each major pollen taxon found at El Valle, Panama. Total pollen concentrations are shown at the right. Taxa attributions are as follows: *Hura* L. (Euphorbiaceae), *Myrica* L. (Myricaceae), *Byrsonima* Rich. ex Kunth (Malpighiaceae), *Alternanthera* Forssk. (Amaranthaceae). Reproduced with permission from Bush and Colinvaux (1990).





Figure 7. The wild ancestor of maize, *Zea mays* subsp. *parriglumis*, growing in the Central Balsas River Valley, Mexico.

and photorespiratory carbon loss (Cowling & Sykes, 1999). In contrast to forest persistence in high rainfall zones, forests were often displaced by savanna/thorny scrub kinds of vegetation during the Pleistocene, where the modern potential vegetation is a highly seasonal forest with annual rainfall of 1.2–2 m a year. Here, the

dry climate, aided by the effects of low CO<sub>2</sub>, resulted in landscapes where forest growth was minimal.

The Central and South American lowland tropical forests are thought to house more plant species than the tropics of Asia and Africa combined (Richardson et al., 2001). There are increasing indications that a good deal

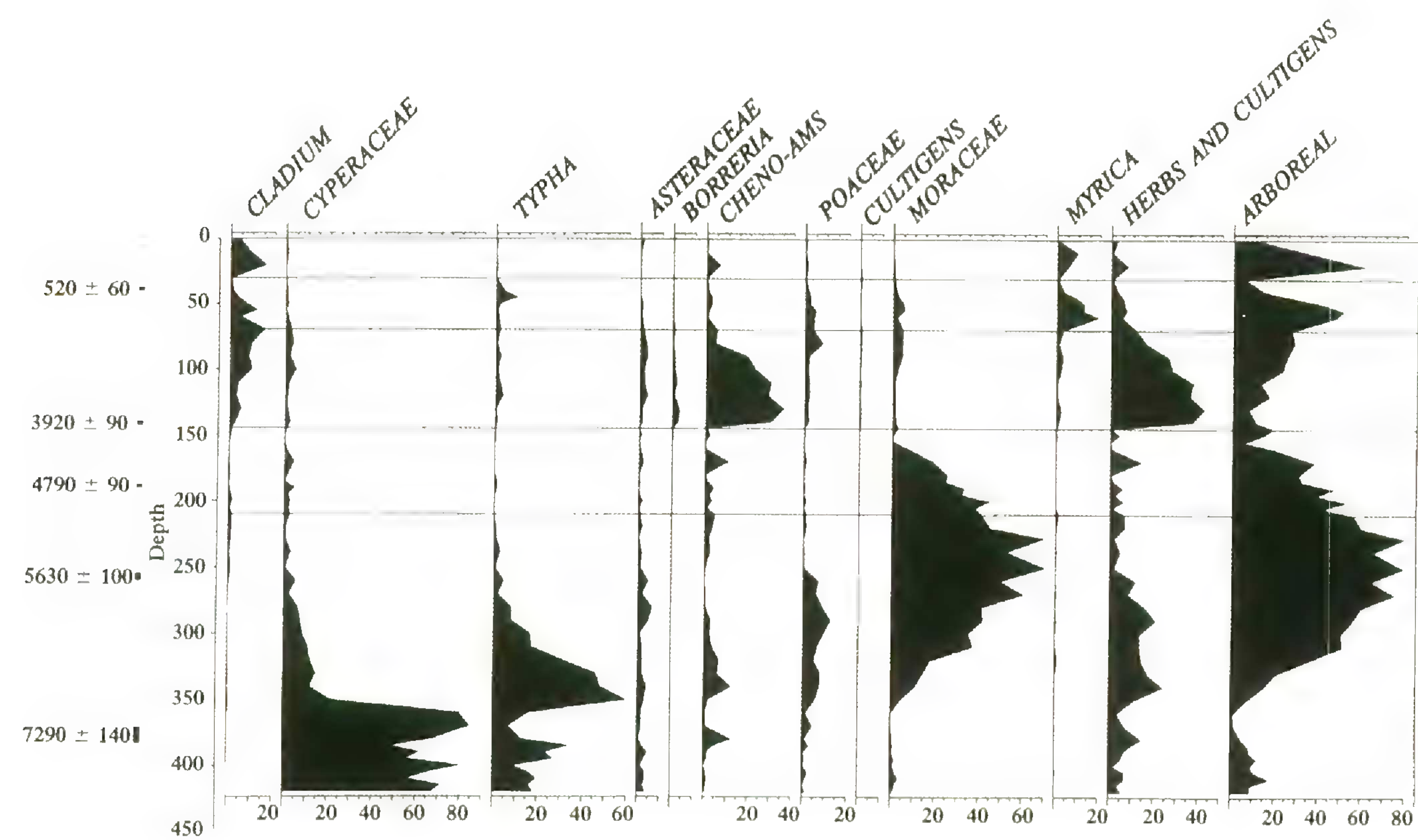


Figure 8. A pollen profile (percentage abundance of pollen at depth in cm below surface; age in <sup>14</sup>C yr. BP) from Cobweb Swamp, Belize. Cultigens are maize, cotton (*Gossypium* L. (Malvaceae)), and chile pepper (*Capsicum* L. (Solanaceae)). Taxa attributions are as follows: *Cladium* P. Browne (Cyperaceae), *Borreria* G. Mey (Rubiaceae). Reproduced with permission from Jones (1991).



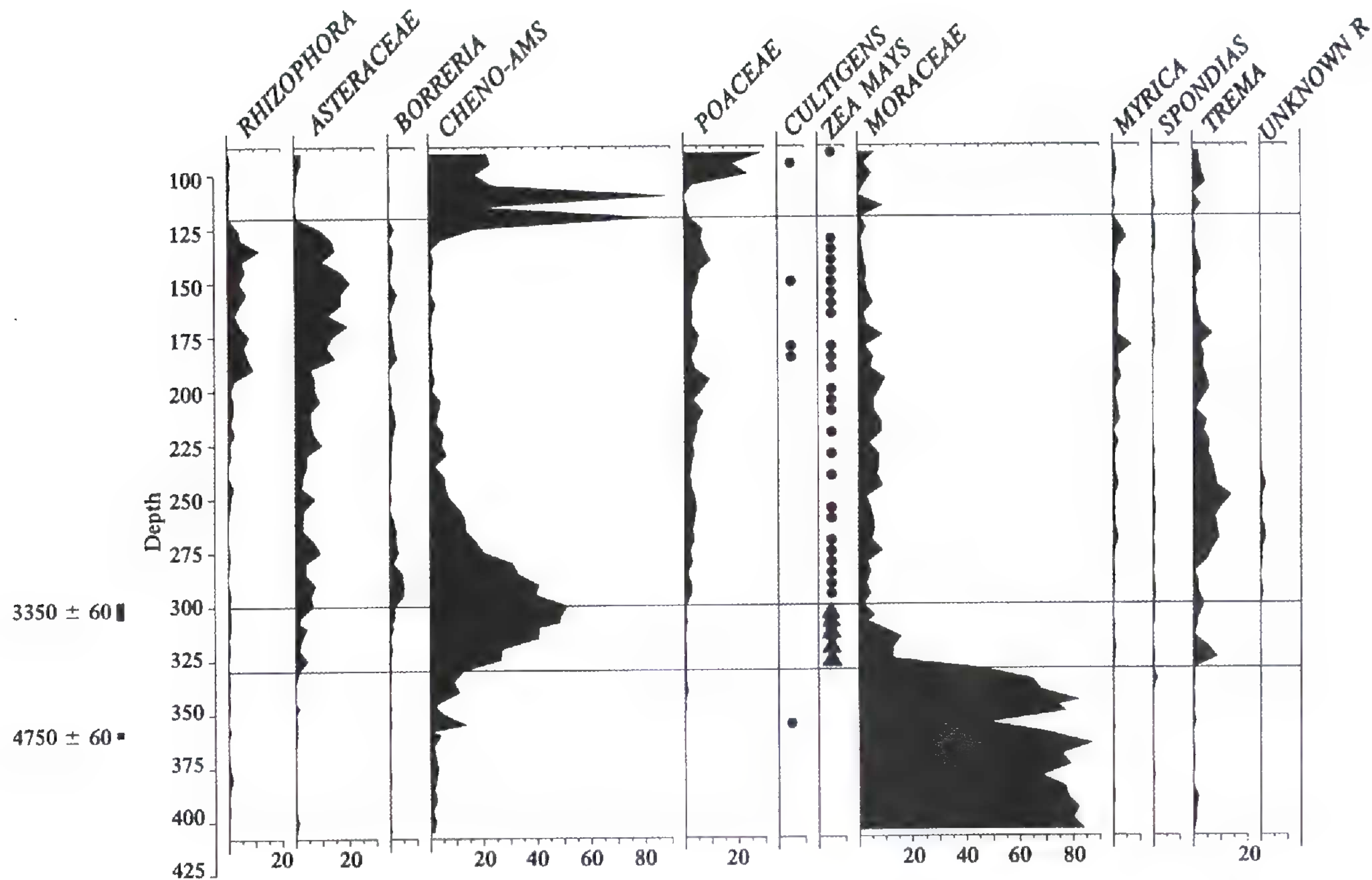


Figure 9. A pollen profile (percentage abundance of pollen at depth in cm below surface; age in <sup>14</sup>C yr. BP) from Kob Swamp, Belize. Cultigens are manioc (*Manihot esculenta* Crantz (Euphorbiaceae)) and cotton. Reproduced with permission from Jones (1994).

of this diversity is pre-Quaternary, perhaps dating to the Eocene (Knapp & Mallet, 2003; Wilf et al., 2003), although recent investigations also show that some tree species of Central and South American seasonally dry forest along with speciose genera of evergreen and other forests in South America probably did speciate during the past few million years (Richardson et al., 2001; Pennington et al., 2004). Whether those speciations occurred in refugia, islands of intact, lowland moist forest surrounded by savannas (Haffer, 1969; Whitmore & Prance, 1987), has not been completely resolved. However, interpretations of Late Pleistocene vegetation that rely on refugial theory appear increasingly less plausible as more paleoecological data accumulate indicating that due to drier conditions postulated refugial areas were nearly devoid of trees, or that these areas contained many colder-adapted taxa presently confined largely to montane forests (Colinvaux et al., 2000; Knapp & Mallet, 2003; Leyden, 1984, 1985).

It is relevant with respect to refugial theory that phytolith evidence from Monte Oscuro, Panama, discussed above, located in a highly seasonal area that was sparsely forested during the Pleistocene, does point to the presence of a number of lowland forest trees such as *Protium* and other Burseraceae, Annonaceae, Chrysobalanaceae, and Moraceae near the lake during the driest times before 10,000 BP. There were almost certainly other tree species present

there and at other similar locations that for various reasons (low pollen productivity or an absence of identifiable phytoliths) are not visible in the paleobotanical records. Some arboreal species may, therefore, have grown in lower densities than is usual today in more mesic pockets on the drier Pleistocene landscapes; for example, they may have been harbored alongside water courses. Studies of modern riparian forests by Meave and Kellman (1994) and others have shown that these linear stretches of vegetation contain a much greater diversity of tree species than was previously thought possible. Sir Ghilleen Prance's (1987) idea that riparian forests were important refuges for lowland forest trees in Amazonia thus has considerable merit, and his view applies equally well to Central America. These findings and ideas on the historical significance of riverine forests should also be remembered by modern planners when they are considering what the sizes, shapes, and species composition of modern reforestation programs should be.

We've learned that the questions we first asked of the historical records—was the Pleistocene vegetation a forest or was it a grassland; were the lowland tropics cooler, or were they drier during an ice age; where did trees go during periods when savannas and scrub lands appear to have dominated landscapes now underneath forest? —were far too simplistic. We have begun to consider more realistic, if increasingly



complicated, Pleistocene scenarios involving the likelihood of different forest facies; the existence of species combinations not presently found together; heterogeneous, even patchy, vegetation across small distance scales; and stretches of forest alongside water courses in regions where forests were significantly reduced that may have held and preserved at least some of the diversity we see today during the past few million years. On average, glacial periods last four to five times longer than interglacials. Hence, during the past two million years, tropical forest plants and animals spent over 80% of their time in, and must have been well accustomed to, a world of lower CO<sub>2</sub>, temperature, and precipitation. Our modern, closed canopied forests appear to be little more than short-term, interglacial floristic associations that coalesced or expanded onto landscapes the last time beginning 11,000 to 10,000 years ago. If the past is indeed the key to the present, then what we have learned about tropical forest history should cause us to look to ancient records for advice concerning, among other things, modeling plant succession following major ecosystem disruptions and predicting and patterning forest regeneration when planning regrowth programs (see also Birks & Birks, 2004, and Wardle et al., 2004).

#### PRE-COLUMBIAN HUMAN IMPACTS ON THE NEOTROPICAL FOREST

During the final 1000 years or so of the Pleistocene, the climate warmed markedly and became substantially wetter and more highly seasonal, and atmospheric concentrations of CO<sub>2</sub> increased, creating conditions in which tropical plants could really flourish. Humans had already arrived in Central and South America by at least 3000 years earlier, as demonstrated by Dillehay's (1997) excavations at Monte Verde, Chile. This work, which overturned the Clovis First paradigm for human colonization of the New World, is accepted as convincing proof of a 13,000 BP human presence in southern South America by a strong consensus of American archaeologists (Meltzer, 1997). At the close of the Pleistocene the human occupants of Central and South America, having spent the late glacial period in cool and dry landscapes where the amount of forest cover was far less than it is today and large, slow-moving, now-extinct game animals abounded, found themselves in surprising and dramatically changing ecological circumstances. Tropical forests, with their far fewer and much smaller animals and more highly dispersed and toxic plant species, were expanding rapidly on landscapes, and new strategies for living in these habitats would become necessary in fairly short

order. One cultural adjustment to the changing ecological circumstances that turned out to be a highly successful adaptation was plant food production.

The transition from a hunting and gathering way of life to one in which human societies became dependent on a food base underwritten by plants they domesticated was accomplished independently in at least eight regions of the Old and New World, including both hemispheres of tropical America, not long after the Pleistocene ended (Diamond, 2002; Piperno & Pearsall, 1998; Kennett & Winterhalder, 2006). It marked the emergence of humans as owners and extraordinary manipulators of their landscapes. In southern Central and northern South America, the best studied regions to date, microfossil (phytolith, starch grain, and pollen) research indicates that the domestication and spread of important native crops like maize, manioc (*Manihot esculenta* Crantz), two species of squash (*Cucurbita moschata* Duchesne and *C. ecuadorensis* H. C. Cutler & Whitaker), arrowroot (*Maranta arundinacea* L.), yams (*Dioscorea trifida* L.f.), and liren (*Calathea allouia* (Aubl.) Lindl.) occurred between 10,000 and 5000 years ago (Bray, 2000; Mora et al., 1991; Pope et al., 2001; Piperno, 2006a; Piperno & Pearsall, 1998; Piperno & Stothert, 2003; Piperno et al., 2000a, b; Pearsall et al., 2003, 2004). Furthermore, together with evidence from molecular biology and botany, this tells us that the most important lowland crops in both Central and South America were originally brought under cultivation and domesticated in the seasonal, not the ever-wet tropical forest, and that the interior of the Amazon Basin had little at all to do with the origins of major subsistence crops (e.g., Matsuoka et al., 2002; Olsen & Schaal, 1999; Piperno & Pearsall, 1998; Piperno, 2006a; Sanjur et al., 2002; Westengen et al., 2005).

Paleoecological data from lakes and large swamps often located near important archaeological sites make it clear that the development and spread of agriculture in the American tropics exerted profound influences on the structure and composition of the vegetation. The numbers of sequences showing human agricultural and other alterations of the lowland tropical forest in Central America during the early and middle Holocene are rapidly increasing, and not all of them can be considered here. It is briefly noted that in addition to the records discussed below, good data also exist from Costa Rica, El Salvador, and coastal Guatemala, as well as from Puerto Rico (see, for example, Clement & Horn, 2001; Dull, 2004; Horn & Sanford, 1992; Arford & Horn, 2004). Virtually everywhere the records show that fire was an important instrument of vegetational modification for hunters and gatherers and people practicing agriculture alike.



At Lake La Yeguada in Panama, a disturbance horizon indicating frequent firing of the forest and small-scale vegetation clearance begins at 11,000 BP after being absent for the first 3000 years of the lake's history, when the climate was much drier (Piperno et al., 1990; Bush et al., 1992; Fig. 5a). The disturbance is represented by a large (several orders of magnitude) and rapid increase of charcoal and plants of forest gaps such as *Heliconia* and grasses, and it is sustained throughout the early Holocene. The initial appearance of the vegetation disturbance coincides with the settlement of the region by Clovis hunters and gatherers. These and later populations who occupied the La Yeguada watershed between 11,000 and 10,000 BP left numerous characteristic stone artifacts, including a projectile point on the shore of the lake itself, that have been found by archaeologists during systematic surveys (Ranere & Cooke, 2003).

More than 70% of the disturbance taxa phytoliths are continually charred from 11,000 to 9000 BP, providing direct indications that they had been fired repeatedly (burnt phytoliths can be easily recognized because they acquire a black coating on their surface; see Piperno, 2006b). Such a scenario would be highly unlikely under burning caused by natural processes because fire return rates in tropical forests documented for the modern era are never that frequent (at La Yeguada, the sampling resolution was often about 100 years). Furthermore, ENSO became a part of the post-Pleistocene climate system only after 6000 to 5000 BP (Moy et al., 2002; Sandweiss et al., 1996), and thus persistent fire events during the early Holocene cannot reasonably be attributed to El Niño dry periods. Hence it appears that early hunters and gatherers repeatedly subjected the forest around La Yeguada to fire and small-scale clearing.

The disturbance at La Yeguada continued unabated and intensified. Then at 7000 BP a marked decline in arboreal and associated species characteristic of older forest growth (which the phytolith record is more adept than pollen at identifying) and continued high frequencies of charcoal indicate the development of slash and burn cultivation. Pollen data, which are very sensitive to a set of woody secondary forest taxa generally not visible in phytolith profiles, such as *Trema*, *Pilea* Lindl., *Ficus* L., and *Cecropia* Loebl., indicate a concurrent substantial increase of such trees (Fig. 5b), confirming the decline in older forest growth recorded by the phytoliths. At 4000 BP, even these pollen types decline greatly, as does charcoal, indicating that an intensification of forest clearance occurred and not many woody taxa were left in the watershed (Fig. 5a, b). Also starting at ca. 7000 BP, when the earliest clear indications of slash and burn cultivation begin, nearby archaeological sites contain



Figure 10. Map of the Central Balsas watershed of Mexico showing the Iguala Valley (grey shading) and coring locations El Venancio and Las Juntas de Río Chico. Tehuacan Valley and Guila Naquitz are archaeological settlements located in the dry highlands where previous research has documented early food production.

the first phytoliths and starch grains from maize and manioc. These records show that crops such as arrowroot and *Cucurbita moschata* were also present by that date (Piperno, 1988, 2006a; Piperno et al., 2000b; Piperno & Pearsall, 1998).

At about 350 BP, when Europeans are known to have first entered the region, a forest resurgence is evident at La Yeguada. It is almost certainly a result of the terrible decimation of indigenous populations that occurred soon after the Spanish contact on account of disease, warfare, and slavery. Hence, the forests around La Yeguada were resilient to long-term prehistoric agriculture. Even so, some of the trees first recorded during the early Holocene do not appear again when indigenous population pressure decreases (e.g., *Protium*), while other taxa, especially forest floor herbs such as the Marantaceae, appear to be present in higher frequencies than they were before the vegetation was fired and cleared.

Similar early manifestations of human firing and clearing of tropical forest have been demonstrated from Mesoamerica to the Amazon Basin. For example, two pollen and charcoal records studied by John Jones from swamps called Kob and Cobweb, located about 55 km apart in northeastern Belize, show an early phase of intensive deforestation resulting from slash and burn agriculture (Jones, 1994; Pohl et al., 1996; Figs. 8, 9). The sites are near major pre-Classic archaeological occupations, and in both cases tree pollen greatly declines and maize is present by 4000 BP. At this time, there are also sudden, major increases of charcoal fragments (not shown) and early successional herbaceous taxa. Among arboreal taxa, even pollen from *Brosimum* Sw. nearly disappears, indicating that the fruit of this tree, called *rámon*, probably was not a primary food source for Classic



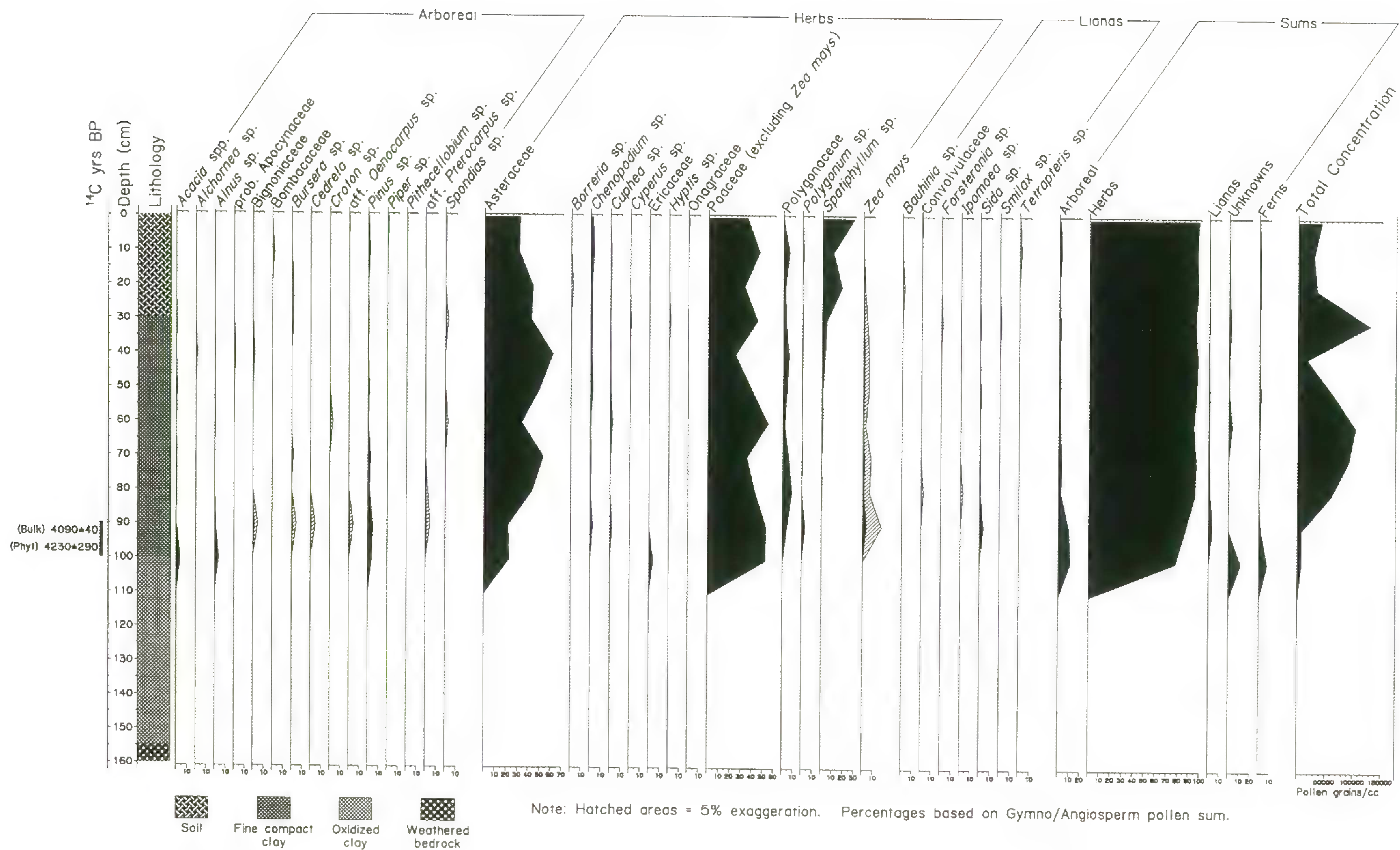


Figure 11. The percentage abundance of pollen of each taxon found in El Venancio, Mexico. Taxa attributions are as follows: *Acacia* L., *Pithecellobium* Mart., and *Pterocarpus* Jacq. (Fabaceae); *Alchornea* Sw. and *Croton* L. (Euphorbiaceae); *Cuphea* P. Browne (Lythraceae); *Cyperus* L. (Cyperaceae); *Forsteronia* G. Mey. (Apocynaceae); *Hyptis* Jacq. (Lamiaceae); *Ipomoea* L. (Convolvulaceae); *Pinus* L. (Pinaceae); *Piper* L. (Piperaceae); *Polygonum* L. (Polygonaceae); *Sida* L. (Malvaceae); *Smilax* L. (Smilacaceae); *Spathiphyllum* Schott (Araceae); *Tetraopteris* Cav. (Malpigiaceae).



Maya peoples, as was thought before Jones's pollen work and other studies showed otherwise (Jones, 1994). As in central Pacific Panama, the fertile soils of northern Belize were able to sustain intensive cultivation for thousands of years. Agricultural activity stops at about the time of European Contact at the Belize sites, but in those cases the forest did not recover. The reasons why are presently unclear.

The seasonal tropical forest of the Río Balsas drainage of Mexico appears, based on molecular studies of modern crops and their nearest wild relatives, to have been an important center of crop plant origins, where maize, the silver-seeded squash (*Cucurbita argyrosperma* Huber), and other plants were domesticated (Matsuoka et al., 2002; Sanjur et al., 2002). However, very little archaeological or paleoecological research has been undertaken there, owing largely to the fact that investigators long assumed that crop plant evolution largely occurred in the dry mountainous zones of the country. Therefore, virtually nothing is known of the earlier segments of pre-Columbian human history (ca. 12,000 BP to 3000 BP) in the Balsas watershed. During the past five years, the author has directed reconnaissance and coring of lakes and swamps in the Central Balsas region, where the modern populations of *Zea mays* subsp. *parviglumis* are genetically closest to maize (Matsuoka et al., 2002; Fig. 10). The Iguala Valley and its environs, located in Guerrero on the eastern side of the Central Balsas drainage, appears to have been a smaller-scale version of the lake district in the Petén, Guatemala, as there are large lakes and numerous other basins that held permanent water until recently (Piperno et al., 2004). The sequences from two of these sites, which date to the Late Pleistocene, are still being investigated in the author's laboratory and cannot yet be discussed in detail.

In the Central Balsas watershed, about 120 km west of Iguala near the town of Ciudad Altamirano, still in Guerrero but close to the border of Michoacán, one large swamp and the remnants of an oxbow lake were located and cored. These sites are called, respectively, El Venancio and Las Juntas de Río Chico (Fig. 10). The elevation of the area is 300 m asl, and annual precipitation is about 1400 mm. The potential vegetation is tropical deciduous forest, but the region is apparently too low-lying and warm to support the growth of teosinte, which has never been collected there. A 1.6 meter-long sequence retrieved from El Venancio has two concordant dates of  $4090 \pm 40$  BP and  $4230 \pm 290$  BP obtained, respectively, from sediments and phytoliths retrieved from the same sediments at a depth of between 90 and 100 cm beneath the surface (b.s.) (Fig. 11). There and up the core to about 30 cm b.s., sediments are dark, organic-

rich, silty clays containing abundant pollen grains and phytoliths. Beneath 100 cm, sediments are organic-poor clays largely devoid of any plant material.

The pollen analysis, carried out by Enrique Moreno of the Smithsonian Tropical Research Institute, shows that by 4000 BP the vegetation contained few trees and was instead dominated by early successional plants indicative of landscape clearing, such as the Poaceae and Asteraceae (Fig. 11). Maize pollen occurs at that time (and is present continually throughout the later portions of the sequence), along with abundant fragments of charcoal (not shown). This picture is repeated at nearby Las Juntas de Río Chico (Fig. 12). Here, a 1.5 meter-long sedimentary sequence shows that the same taxa indicative of landscape clearing present at El Venancio by 4000 BP dominate the pollen assemblages found at a depth of 110 to 120 cm b.s., dated to  $3050 \pm 40$  BP. Maize pollen and abundant charcoal particles occur here. Sediments beneath 120 cm b.s. contain relatively few pollen grains, making it difficult to interpret the vegetation with the degree of confidence possible in stratigraphically higher deposits. It can be said that the basal-most pollen, which on the basis of estimates derived from sedimentation rates probably dates to about 4000 BP, is mostly from grasses, and there is no large spike of fern spores that would indicate differential degradation of pollen grains (the pine pollen is almost certainly a result of long distance transport). Importantly, there are also abundant charcoal particles in the deepest sediments.

We thus have our first indications that in the Central Balsas region, thought now to be a cradle of agriculture in Mesoamerica and the hearth of maize, agricultural systems using maize that resulted in intensive forest clearing have considerable antiquity. The few trees and lianas remaining on the landscape at 4000 BP (*Cedrela* P. Browne, *Spondias*, *Bombacaceae*, *Bauhinia* L., palms such as *Oenocarpus* Mart.) provide but a small hint of the species-rich forest that existed before humans burned and cleared the vegetation.

A discussion of the South American paleoecological records that speak to ancient human modification of the environment for agricultural and other practices is beyond the scope of this paper. However, one important pollen record studied by the prominent Colombian paleoecologist, Luisa Herrera, and her colleagues should be mentioned (Mora et al., 1991). The sequence comes from the wet evergreen forest of the now-remote middle stretches of the Río Caquetá in the center of the Colombian Amazon (annual precipitation  $> 3000$  mm). It shows clearly that by 4700 BP a slash and burn system of agriculture using maize, manioc, and other crops was well established



LAS JUNTAS DE RIO CHICO  
POLLEN DIAGRAM

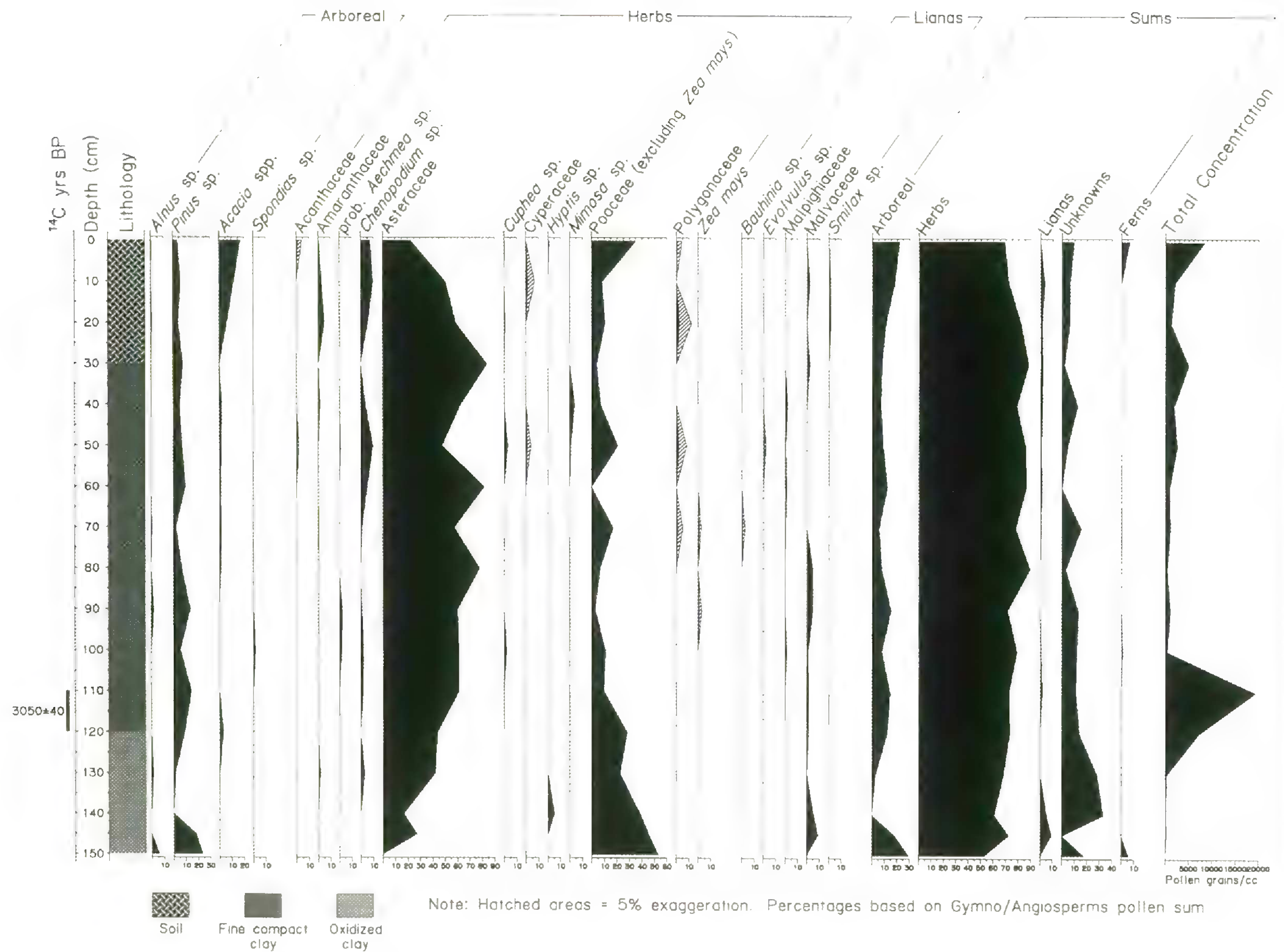


Figure 12. The percentage abundance of pollen of each taxon found in Las Juntas de Río Chico, Mexico. Taxa attributions are as follows: *Aechmea* Ruiz & Pavón (Bromeliaceae); *Evolvulus* L. (Convolvulaceae); *Mimosa* L. (Fabaceae).



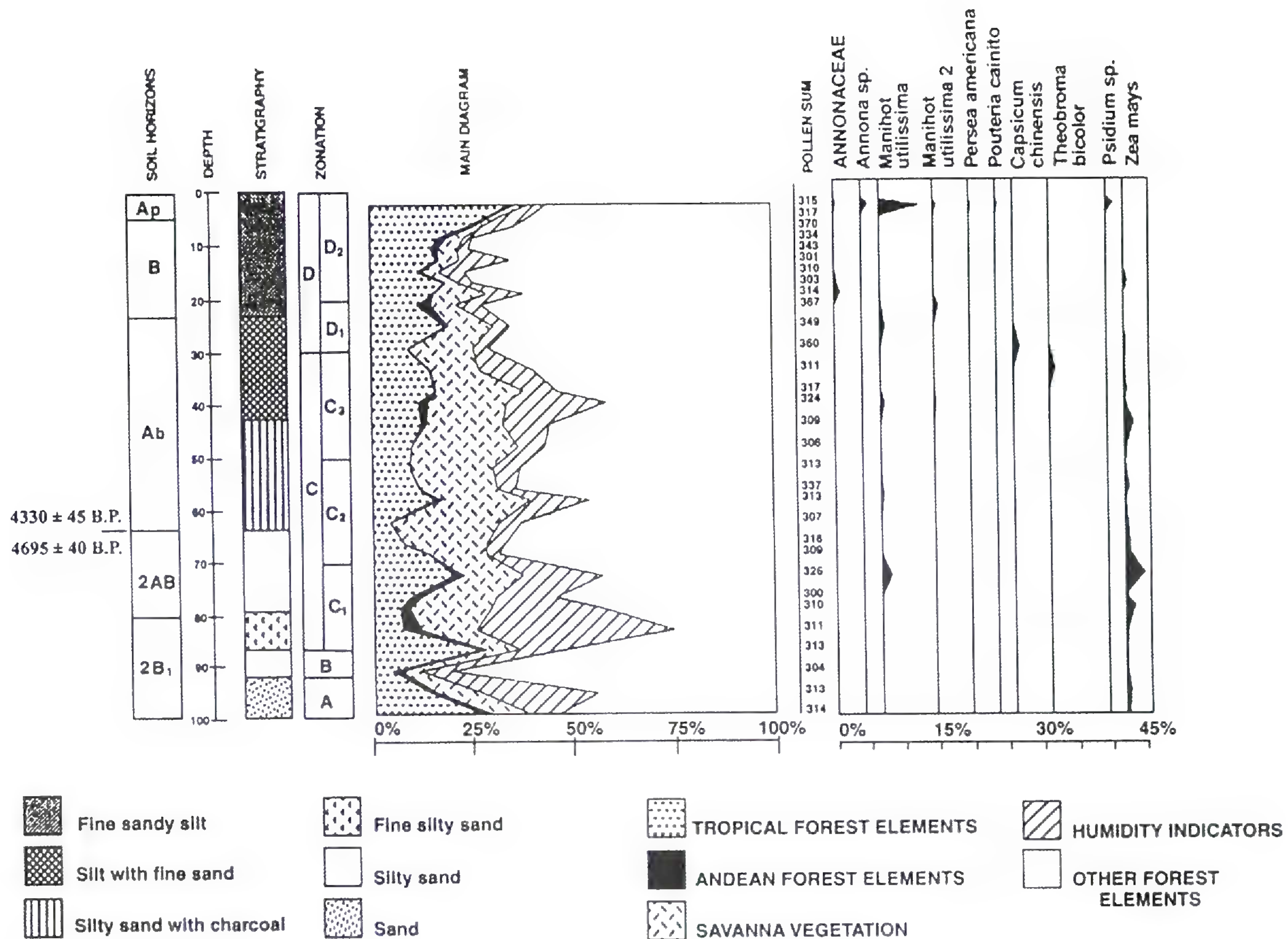


Figure 13. Pollen (the percentage of pollen of each taxon) and charcoal profiles found in the Río Caquetá region of the Colombian Amazon. Taxa attributions are as follows: *Annona* L. (Annonaceae), *Manihot utilissima* Pohl (Euphorbiaceae), *Persea americana* Mill. (Lauraceae), *Pouteria cainito* (Ruiz & Pavón) Radlk. (Sapotaceae), *Capsicum chinense* Jacq. (Solanaceae), *Theobroma bicolor* Bonpl. (Sterculiaceae), *Psidium* L. (Myrtaceae). Reproduced with permission from Mora et al. (1991).



(Fig. 13). By this time, grasses and other field weeds had supplanted the species-rich forest. As in the Central American sequences, presence of abundant fragments of charcoal at 4700 BP testify that fire played an important role in field preparation. At about 775 years ago, when associated archaeological data indicate the site was abandoned by its human occupants, higher frequencies of trees returned and burning ceased. This record from the Colombian Amazon can be contrasted to those from three distinct watersheds in the "Hill of Six Lakes" region, located in wet evergreen forest in northern Brazil where annual precipitation is greater than 3000 mm (Colinvaux et al., 1996; Bush et al., 2004). These sequences demonstrate that few forest fires and no recognizable human vegetational modification occurred in the area during a very long time period stretching from more than 40,000 years ago to the modern era.

Sauer (1958) argued that humankind's successful adaptation to the tropical forest, especially the seasonally dry one, was aided greatly by the use of fire. He presciently predicted that because Neotropical trees are thin-barked and thus poorly insulated, having had apparently a short evolutionary history with fire, early hunters and gatherers and farmers alike could use fire as a highly effective tool for exploiting the forest. This made it possible to kill trees easily and create substantial openings or enlarge existing open areas without having to depend on a sophisticated stone tool technology (Sauer, 1958). In Panama, the Colombian Amazon, and other areas not discussed here where paleoecological records testify to the appearance of slash and burn cultivation several millennia and more ago, associated archaeological data indicate that stone axes were not commonly used before 3000 BP (Piperno & Pearsall, 1998).

#### SUMMARY: WHAT HAVE WE LEARNED ABOUT ANCIENT HUMAN IMPACTS ON NEOTROPICAL VEGETATION?

Human cultures had profound effects on the structure and composition of the lowland tropical forest long before Europeans arrived. Human-induced perturbations were often greater and more widespread than those brought about by Pleistocene climatic and other physical factors. Many arboreal and even herbaceous taxa were in large or smaller part removed from landscapes that were underneath indigenous agricultural systems. Other plants experienced range extensions as they were widely dispersed together with crop plant species, or were otherwise exchanged between human cultures, experimented with, and grown outside of their native habitats. Existing records also suggest that different species and plant commu-

nities had contrasting regenerative capacities following severe disruption, as they do today. Without paleoecological data it might be difficult to know how much of any extant forest was truly very old or not an artificial product of human intervention and subsequent abandonment.

Although we now understand that early peoples substantially altered their landscapes, we should not assume that every tract of lowland tropical forest was heavily settled and disturbed during the prehistoric era. With little doubt, variability in land use patterns resulting from the inherent fertility of soils, type of agriculture practiced (root/tree- vs. seed-based), and associated human population densities resulted in differential impacts on vegetation. The contrasting records from the Hill of Six Lakes in Brazil and the Río Caquetá region of the Colombian Amazon discussed above are but two examples (see Piperno & Becker, 1996, and Bush et al., 2000, for three others from the Brazilian Amazon).

The timing and duration of landscape modification would also have varied depending on whether a region was a cradle of crop plant evolution or otherwise witnessed early developments of agricultural systems through participation in the initial dispersals of domesticated plants, as occurred in Central Pacific Panama, for example. One might suspect, then, that highly seasonal tropical forests, which on present evidence were the geographic cradles of origin for many staple seed and root crops of the Neotropics, were more greatly affected over more protracted time scales than were forests in wet, aseasonal, and poorly soiled regions. While these are reasonable suggestions that accord well with available information, data from many regions are still few and there is much to be learned.

Unlike the thinking that prevailed in human studies little more than 20 years ago, many anthropologists now decline to argue that modern land use practices in the tropics by small-scale, politically autonomous indigenous societies preserve or increase plant diversity, or that there is an inherent conservation ethic that simpler human societies still adhere to (see Alcorn, 1996, Redford & Padoch, 1992, and Alvard, 1995, for good discussions of these issues). I doubt that these ideas constitute accurate assessments of human relationships with, and impacts on, natural resources at any moment in time. None of the now substantial paleoecological records indicate they were true in the past. If Europeans had not arrived little more than 500 years ago and tragically all but ended indigenous life in many areas of Central and South America, it is very much an open question as to how sustainable intensifying or even maintaining existing agricultural practices would have been under ever-



increasing human population densities, even with the use of relatively simple technologies (stone tools and fire) as instruments of forest clearing. Archaeological records from the tropics and elsewhere also tell stories of over-exploitation of marine and other resources during the prehistoric era (e.g., Jones et al., 2004; Mannino & Thomas, 2002; Porcasi et al., 2000; Stahl, 1996; Steadman, 1995). Moreover, rigorous studies of modern indigenous resource use in tropical South America make it clear that short-term self-interest and a desire to capture game in an energetically efficient manner structure hunting and other subsistence pursuits much more so than does a long-term interest in conserving resources (e.g., Alvard, 1993, 1995; Winterhalder & Lu, 1997).

In order to better preserve and protect the remaining forests, we have to straightforwardly assess past and present human behavior, its proclivities, and its goals. At the very least, we should more carefully define what we mean by the word conservation when we describe modern indigenous resource use (is it a designed attempt to preserve an existing biomass and diversity, or an epiphenomenal by-product of factors such as low human population and high prey densities?), no matter how sustainable the resource usage appears to be (see Alvard, 1993, and Smith & Wishnie, 2000, for excellent discussions of this issue).

Finally, there is little doubt now that the views originally taken by Donald Lathrap and Carl Sauer (Lathrap, 1970, 1973b; Sauer, 1936, 1947, 1950) concerning the importance of the lowland Neotropical forest in the emergence and spread of domesticated species, the development of effective agricultural systems, and the flourishing of cultural life in general, were correct in many aspects. In fact, as Lathrap had predicted, the origins of New World pottery occurred in the heart of Amazonia 7000 years ago (Roosevelt et al., 1991), and the first permanent, agricultural villages were created by people who lived in the seasonal forests of southwest Ecuador 5000 years ago (Lathrap et al., 1975; Pearsall et al., 2004). Newer explorations in the Brazilian Amazon have documented that beginning a few centuries before the time of Christ, very large, dense, and permanent human settlements existed in the middle to lower stretches of the main Amazon river channel and Upper Xingu region, which are now sparsely populated and under forest cover (Heckenberger et al., 1999, 2003). As with the forces associated with “development” today, these prehistoric advances probably came with negative consequences for the native flora and fauna. Profound human alteration of the tropical landscape with substantial loss of biodiversity is hardly new, but we are the first societies with the wherewithal to do something about it.

#### Literature Cited

- Alcorn, J. B. 1996. Is biodiversity conserved by indigenous peoples? Pp. 234–238 in S. K. Jain (editor), *Ethnobiology in Human Welfare*. Deep Publications, New Delhi.
- Alvard, M. S. 1993. Testing the “ecologically noble savage” hypothesis: Interspecific prey choice by Piro hunters of Amazonian Peru. *Human Ecol.* 21: 355–387.
- . 1995. Intraspecific prey choice by Amazonian hunters. *Curr. Anthropol.* 36: 789–818.
- Arford, M. R. & S. P. Horn. 2004. Pollen evidence of the earliest maize agriculture in Costa Rica. *J. Latin Amer. Geogr.* 3: 108–115.
- Bailey, R. C. et al. (+ 5 authors). 1989. Hunting and gathering in tropical rain forest: Is it possible? *Amer. Anthropol.* 91: 59–82.
- Barnola, J. M., D. Raynaud, Y. S. Korotkevich & C. Lorius. 1987. Vostoc ice core provides 160,000-year record of atmospheric CO<sub>2</sub>. *Nature* 329: 408–414.
- Bartlett, A. S. & E. S. Barghoorn. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years. Pp. 203–299 in A. Graham (editor), *Vegetation and Vegetational History of Northern Latin America*. Elsevier, Amsterdam.
- Birks, H. J. B. & H. H. Birks. 2004. The rise and fall of forests. *Science* 305: 484–485.
- Bray, W. 2000. Ancient food for thought. *Nature* 408: 145–146.
- Bush, M. B. & P. A. Colinvaux. 1988. A 7000 year-old pollen record from the Amazon lowlands. *Vegetatio* 76: 141–154.
- & ———. 1990. A pollen record of a complete glacial cycle from lowland Panama. *J. Veg. Sci.* 1: 105–118.
- , D. R. Piperno & P. A. Colinvaux. 1989. A 6000 year history of Amazonian maize cultivation. *Nature* 340: 303–305.
- et al. (+ 6 authors). 1992. A 14,300-yr paleoecological profile of a lowland tropical lake in Panama. *Ecol. Mono.* 62: 251–275.
- Bush, M. B., M. C. Miller, P. E. De Oliveira & P. A. Colinvaux. 2000. Two histories of environmental change and human disturbance in eastern lowland Amazonia. *The Holocene* 10: 543–553.
- , P. E. De Oliveira, P. A. Colinvaux, M. C. Miller & J. E. Morenov. 2004. Amazonian paleoecological histories: One hill, three watersheds. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 214: 347–358.
- Clement, R. M. & S. P. Horn. 2001. Pre-Columbian land use history in Costa Rica: A 3000-year record of forest clearance, agriculture, and forest from Laguna Zoncho. *The Holocene* 11: 419–426.
- Colinvaux, P. A., P. E. De Oliveira, P. E. Moreno, M. C. Miller & M. B. Bush. 1996. A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science* 274: 85–88.
- , ——— & M. B. Bush. 2000. Amazonian and Neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. *Quatern. Sci. Rev.* 19: 141–169.
- Cooke, R. G. & A. J. Ranere. 1984. The “Proyecto Santa María”: A multidisciplinary analysis of prehistoric adaptations to a tropical watershed in Panama. Pp. 3–30 in F. W. Lange (editor), *Recent Developments in Isthmian Archaeology*. British Archaeological Reports International Series 212, Oxford.
- Cowling, S. A. & M. T. Sykes. 1999. Physiological significance of low atmospheric CO<sub>2</sub> for plant-climate interactions. *Quatern. Res.* 52: 237–242.



- Curtis, J. H., M. Brenner & D. A. Hodell. 1999. Climate change in the Lake Valencia Basin, Venezuela, 12600 yr BP to Present. *The Holocene* 9: 609–619.
- Deevey, E. S. et al. (+ 5 authors). 1979. Mayan urbanism: Impact on a tropical karst environment. *Science* 206: 298–306.
- Diamond, J. 2002. Evolution, consequences, and future of plant and animal domestication. *Nature* 418: 700–707.
- Dillehay, T. D. 1997. Monte Verde: A Late Pleistocene Settlement in Chile, Vol. 2: The Archaeological Context and Interpretation. Smithsonian Institution Press, Washington, DC.
- . 2000. *The Settlement of the Americas. A New Prehistory*. Basic Books, New York.
- Dods, R. R. 2002. The death of Smokey Bear: The ecodisaster myth and forest management practices in prehistoric North America. *World Archaeol.* 33: 475–487.
- Doebley, J. 1990. Molecular evidence and the evolution of maize. *Econ. Bot.* 44(3 supplement): 6–27.
- Dull, R. A. 2004. An 8000-year record of vegetation, climate, and human disturbance from the Sierra de Apaneca, El Salvador. *Quatern. Res.* 61: 159–167.
- Fischer, A. 1960. Latitudinal variations in organic diversity. *Evolution* 14: 64–81.
- Grimm, E. C., S. Lozano-García, H. Behling & V. Markgraf. 2001. Holocene vegetation and climate variability in the Americas. Pp. 325–370 in V. Markgraf (editor), *Interhemispheric Climate Linkages*. Academic Press, San Diego.
- Guilderson, T. P., R. G. Fairbanks & J. L. Rubenston. 1994. Tropical temperature variations since 20,000 years ago: Modeling interhemispheric climate change. *Science* 263: 663–665.
- Haffer, J. 1969. Speciation in Amazonian forest birds. *Science* 165: 131–137.
- Hart, T. & J. Hart. 1986. The ecological basis of hunter-gatherer subsistence in African rain forests: The Mbuti of Eastern Zaire. *Human Ecol.* 14: 29–55.
- Heckenberger, M. J., J. B. Peterson & E. G. Neves. 1999. Village size and permanence in Amazonia: Two archaeological examples from Brazil. *Latin Amer. Antiquity* 10: 353–376.
- et al. (+ 6 authors). 2003. Amazonia 1492: Pristine forest or cultural parkland? *Science* 301: 1710–1714.
- Hodell, D. A. et al. (+ 6 authors). 1991. Reconstruction of Caribbean climate change over the past 10,500 years. *Nature* 352: 790–792.
- Horn, S. P. & R. L. Sanford Jr. 1992. Holocene fires in Costa Rica. *Biotropica* 24: 354–361.
- Huang, Y. et al. (+ 5 authors). 2001. Climate change as the dominant control on glacial-interglacial variations in  $C_3$  and  $C_4$  plant abundance. *Science* 293: 1647–1651.
- Jones, J. G. 1991. Pollen Evidence of Prehistoric Forest Modification and Maya Cultivation in Belize. Unpublished Ph.D. Dissertation, Department of Anthropology, Texas A&M University, College Station.
- . 1994. Pollen evidence for early settlement and agriculture in northern Belize. *Palynology* 18: 205–211.
- Jones, T. L., W. R. Hildebrandt, D. J. Kennett & J. F. Porcasi. 2004. Prehistoric marine mammal overkill in the northeastern Pacific: A review of some new evidence. *J. Calif. Great Basin Anthropol.* 24: 69–80.
- Kennett, D. & B. Winterhalder (editors). 2006. *Behavioral Ecology and the Transition to Agriculture*. Univ. California Press, Berkeley.
- Knapp, S. & J. Mallet. 2003. Refuting refugia? *Science* 300: 71–72.
- Lathrap, D. W. 1970. *The Upper Amazon*. Praeger Publishers, New York.
- . 1973a. Gifts of the cayman: Some thoughts on the subsistence basis of Chavin. Pp. 91–105 in D. W. Lathrap & J. Douglas (editors), *Variation in Anthropology: Essays in Honor of John McGregor*. Illinois Archaeological Survey, Urbana.
- . 1973b. The antiquity and importance of long distance trade relationships in the moist tropics of pre-Columbian South America. *World Archaeol.* 5: 170–186.
- , D. Collier & H. Chandra. 1975. *Ancient Ecuador: Culture, Clay, and Creativity, 3000–300 B.C.* Field Museum of Natural History, Chicago.
- Ledru, M.-P., J. Bertaux, A. Sifeddine & K. Suguio. 1998. Absence of Last Glacial Maximum records in lowland tropical forests. *Quatern. Res.* 49: 233–237.
- Leyden, B. 1984. Guatemalan forest synthesis after Pleistocene aridity. *Proc. Natl. Acad. Sci. U.S.A.* 81: 4856–4859.
- . 1985. Late Quaternary aridity and Holocene moisture fluctuations in the Lake Valencia Basin, Venezuela. *Ecology* 66: 1279–1295.
- . 1987. Man and climate in the Maya lowlands. *Quatern. Res.* 28: 407–414.
- , M. Brenner, D. A. Hodell & J. H. Curtis. 1993. Late Pleistocene climate in the Central American lowlands. Pp. 165–178 in P. K. Swart, K. C. Lohmann, J. McKenzie & S. Savin (editors), *Climate Change in Continental Isotopic Records*. Geophysical Monograph 78. American Geophysical Union, Washington, DC.
- Livingstone, D. A. 1975. Late Quaternary climatic change in Africa. *Annual Rev. Ecol. Syst.* 6: 249–280.
- Mangelsdorf, P. C. 1953. Review of "Agricultural Origins and Dispersals" by Carl O. Sauer. *Amer. Antiquity* 19: 86–90.
- , R. S. MacNeish & G. R. Willey. 1964. Origins of agriculture in Middle America. Pp. 427–445 in R. C. West (editor), *Handbook of Middle American Indians: Natural Environment and Early Cultures*, Vol. 1. Univ. Texas Press, Austin.
- Mannino, M. A. & K. D. Thomas. 2002. Depletion of a resource? The impact of prehistoric human foraging on intertidal mollusc communities and its significance for human settlement, mobility, and dispersal. *World Archaeol.* 33: 452–474.
- Martin, P. S. 1964. Paleoclimatology and a tropical pollen profile. Pp. 319–323 in Report of the VIth International Congress on Quaternary (Warsaw 1961), Vol II: Palaeo-Climatological Section. Lodz.
- Matsuoka, Y. et al. (+ 5 authors). 2002. A single domestication for maize shown by multilocus microsatellite genotyping. *Proc. Natl. Acad. Sci. U.S.A.* 99: 6080–6084.
- Mayle, F. E. & D. J. Beerling. 2004. Late Quaternary changes in Amazonian ecosystems and their implications for global carbon cycling. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 214: 11–25.
- Meave, J. & M. Kellman. 1994. Maintenance of rain forest diversity in riparian forests of tropical savannas: Implications for species conservation during Pleistocene drought. *J. Biogeogr.* 21: 121–153.
- Meggers, B. J. 1954. Environmental limitations on the development of culture. *Amer. Anthropol.* 56: 801–824.
- . 1971. *Amazonia: Man and Culture in a Counterfeit Paradise*. Aldine, Chicago.
- Meltzer, D. J. 1997. Monte Verde and the Pleistocene peopling of the Americas. *Science* 276: 754–755.



- , J. M. Adovasio & T. D. Dillehay. 1994. On a Pleistocene human occupation at Pedra Furada, Brazil. *Antiquity* 68: 695–714.
- Mora, S. C., L. F. Herrera, I. Cavelier & C. Rodríguez. 1991. Cultivars, Anthropogenic Soils and Stability. Univ. Pittsburgh Latin Amer. Archaeol. Rep. No. 2. Univ. Pittsburgh, Dept. Anthropol., Pittsburgh.
- Moy, C. M., G. O. Seltzer, D. T. Rodbell & D. M. Anderson. 2002. Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature* 420: 162–165.
- Olsen, K. M. & B. A. Schaal. 1999. Evidence on the origin of cassava: Phylogeography of *Manihot esculenta*. *Proc. Natl. Acad. Sci. U.S.A.* 96: 5586–5591.
- Pearsall, D. M. 1978. Phytolith analysis of archaeological soils: Evidence for maize cultivation in formative Ecuador. *Science* 199: 177–178.
- , K. Chandler-Ezell & A. Chandler-Ezell. 2003. Identifying maize in Neotropical sediments and soils using cob phytoliths. *J. Archaeol. Sci.* 30: 611–627.
- , ——— & J. A. Zeidler. 2004. Maize in ancient Ecuador: Results of residue analysis of stone tools from the Real Alto site. *J. Archaeol. Sci.* 31: 423–442.
- Peltier, W. R. & L. P. Solheim. 2004. The climate of the earth at the Last Glacial Maximum: Statistical equilibrium state and a mode of internal variability. *Quatern. Sci. Rev.* 23: 335–357.
- Pennington, R. T. et al. (+ 5 authors). 2004. Historical climate change and speciation: Neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Philos. Trans. Ser. B.* 359: 515–538.
- Piperno, D. R. 1985a. Phytolith analysis and tropical paleoecology: Production and taxonomic significance of siliceous forms in New World plant domesticates and wild species. *Rev. Palaeobot. Palynol.* 45: 185–228.
- . 1985b. Phytolith taphonomy and distributions in archaeological sediments from Panama. *J. Archaeol. Sci.* 12: 247–267.
- . 1988. *Phytolith Analysis: An Archaeological and Geological Perspective*. Academic Press, San Diego.
- . 2006a. A behavioral ecological approach to the origins of plant cultivation and domestication in the seasonal tropical forests of the New World. *In* D. Kennett & B. Winterhalder (editors), *Behavioral Ecology and the Transition to Agriculture*. Univ. California Press.
- . 2006b. *Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists*. AltaMira Press, Lanham, Maryland.
- & P. Becker. 1996. Vegetational history of a site in the central Amazon Basin derived from phytolith and charcoal records from natural soils. *Quatern. Res.* 45: 202–209.
- & J. Jones. 2003. Paleoecological and archaeological implications of a late Pleistocene/early Holocene record of vegetation and climate from the Pacific coastal plain of Panama. *Quatern. Res.* 59: 79–87.
- & D. M. Pearsall. 1998. *The Origins of Agriculture in the Lowland Neotropics*. Academic Press, San Diego.
- & K. E. Stothert. 2003. Phytolith evidence for early Holocene *Cucurbita* domestication in Southwest Ecuador. *Science* 299: 1054–1057.
- , M. B. Bush & P. A. Colinvaux. 1990. Paleoenvironments and human occupation in Late-Glacial Panama. *Quatern. Res.* 33: 108–116.
- , ——— & ———. 1991a. Paleoecological perspectives on human adaptation in Central Panama. I. The Pleistocene. *Geoarchaeology* 6: 210–226.
- , ——— & ———. 1991b. Paleoecological perspectives on human adaptation in Central Panama. II. The Holocene. *Geoarchaeology* 6: 227–250.
- , ——— & ———. 1992. Patterns of articulation of culture and the plant world in prehistoric Panama: 11,500 BP–3000 BP. Pp. 109–127 *in* O. R. Ortiz-Troncoso & T. Van der Hammen (editors), *Archaeology and Environment in Latin America*. Universiteit van Amsterdam, Amsterdam.
- , A. J. Ranere, I. Holst & P. Hansell. 2000a. Starch grains reveal early root crop horticulture in the Panamanian tropical forest. *Nature* 407: 894–897.
- , I. Holst, T. C. Andres & K. E. Stothert. 2000b. Phytoliths in *Cucurbita* and other Neotropical Cucurbitaceae and their occurrence in early archaeological sites from the lowland American tropics. *J. Archaeol. Sci.* 27: 193–208.
- et al. (+ 6 authors). 2004. Environmental and Agricultural History in the Central Balsas Watershed, Mexico: Results of Preliminary Research. Paper read at the Annual Meeting of the Society for American Archaeology, Montreal, Canada.
- Pohl, M. D. et al. (+ 10 authors). 1996. Early agriculture in the Maya lowlands. *Latin Amer. Antiquity* 7: 355–372.
- Pope, K. O. et al. (+ 6 authors). 2001. Origin and environmental setting of ancient agriculture in the lowlands of Mesoamerica. *Science* 292: 1370–1373.
- Porcasi, J. F., T. L. Jones & L. M. Raab. 2000. Trans-Holocene marine mammal exploitation on San Clemente Island, California: A tragedy of the commons revisited. *J. Anthropol. Archaeol.* 19: 200–220.
- Prance, G. T. 1987. Vegetation. Pp. 28–45 *in* T. C. Whitmore & G. T. Prance (editors), *Biogeography and Quaternary History in Tropical America*. Clarendon Press, Oxford.
- Ranere, A. J. & R. G. Cooke. 2003. Late glacial and early Holocene occupation of Central American tropical forests. Pp. 210–248 *in* J. Mercader (editor), *Under the Canopy: The Archaeology of Tropical Rain Forests*. Rutgers Univ. Press, New Brunswick.
- Redford, K. H. & C. Padoch. 1992. *Conservation of Neotropical Forests*. Columbia Univ. Press, New York.
- Richardson, J. E., R. T. Pennington, T. D. Pennington & P. M. Hollingsworth. 2001. Rapid diversification of a species-rich genus of Neotropical rain forest trees. *Science* 293: 2242–2245.
- Roosevelt, A. C., R. A. Housley, M. I. Da Silveira, S. Maranca & R. Johnson. 1991. Eighth millennium pottery from a prehistoric shell midden in the Brazilian Amazon. *Science* 254: 1621–1624.
- Sage, R. F. 1995. Was low atmospheric CO<sub>2</sub> during the Pleistocene a limiting factor for the origin of agriculture? *Global Change Biol.* 1: 93–106.
- Sandweiss, D. H., J. B. Richardson III, E. J. Reitz, H. B. Rollins & K. A. Maasch. 1996. Geoarchaeological evidence from Peru for a 5000 years B.P. onset of El Niño. *Science* 273: 1531–1533.
- Sanjurjo, O., D. R. Piperno, T. C. Andres & L. Wessell-Beaver. 2002. Phylogenetic relationships among domesticated and wild species of *Cucurbita* (Cucurbitaceae) inferred from a mitochondrial gene: Implications for crop plant evolution and areas of origin. *Proc. Natl. Acad. Sci. U.S.A.* 99: 535–540.
- Sauer, C. O. 1936. American agricultural origins: A consideration of nature and agriculture. Pp. 279–298 *in* R. H. Lowie (editor), *Essays in Anthropology in Honor of A. L. Kroeber*, Univ. California Press, Berkeley.
- . 1947. Early relations of man to plants. *Geogr. Rev.* (New York) 37: 1–25.



- . 1950. Cultivated plants of South and Central America. Pp. 487–543 in J. Steward (editor), *Handbook of South American Indians*. Bureau of American Ethnology Bulletin 143, Vol. 6. U.S. Government Printing Office, Washington, D. C.
- . 1952. *Agricultural Origins and Dispersals*. American Geographical Society, New York.
- . 1958. Man in the ecology of tropical America. *Proceedings of the Ninth Pacific Science Congress*, Bangkok, Thailand 20: 104–110.
- Slobodkin, L. B. & H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. *Brookhaven Symposium in Biology* 22: 82–95.
- Smith, E. A. & M. Wishnie. 2000. Conservation and subsistence in small-scale societies. *Annual Rev. Anthropol.* 29: 493–524.
- Sponsel, L. E. 1989. Farming and foraging: A necessary complementarity in Amazonia? Pp. 37–45 in S. Kent (editor), *Farmers as Hunters: The Implications of Sedentism*. Cambridge Univ. Press, Cambridge, Massachusetts.
- Stahl, P. W. 1996. Holocene biodiversity: An archaeological perspective from the Americas. *Annual Rev. Anthropol.* 25: 105–26.
- Steadman, D. 1995. Prehistoric extinctions of Pacific Island birds: Biodiversity meets zooarchaeology. *Science* 267: 1123–1131.
- Van der Hammen, T. & E. Gonzalez. 1960. Upper Pleistocene and Holocene climate and vegetation of the Sabana de Bogotá (Colombia, South America). *Leidse Geol. Meded.* 25: 126–315.
- & H. Hooghiemstra. 2000. Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. *Quatern. Sci. Rev.* 19: 725–742.
- Wardle, D. A., L. R. Walker & R. D. Bardgett. 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305: 509–513.
- Webb, R. S., R. D. Rind, S. J. Lehman, R. J. Healy & D. Sigman. 1997. Influence of ocean heat transport on the climate of the Last Glacial Maximum. *Nature* 385: 695–699.
- Westengen, O. T., Z. Huamán & M. Heun. 2005. Genetic diversity and geographic pattern in early South American cotton domestication. *Theor. Appl. Genet.* 110: 392–402.
- Whitmore, T. C. & G. T. Prance (editors). 1987. *Biogeography and Quaternary History in Tropical America*. Clarendon Press, Oxford.
- Wilf, P. et al. (+ 5 authors). 2003. High plant diversity in Eocene South America: Evidence from Patagonia. *Science* 300: 122–125.
- Winterhalder, B. & F. Lu. 1997. A forager-resource population ecology model and implications for indigenous conservation. *Conservation Biol.* 11: 1354–1364.